DINO FEST

Edited by

Gary D. Rosenberg and Donald L. Wolberg

Proceedings of a conference for the general public
held March 24-26, 1994 at Indianapolis, Indiana
Hosted by
The Department of Geology
Indiana University-Purdue University at Indianapolis.

THE PALEONTOLOGICAL SOCIETY
SPECIAL PUBLICATION NO. 7
1994

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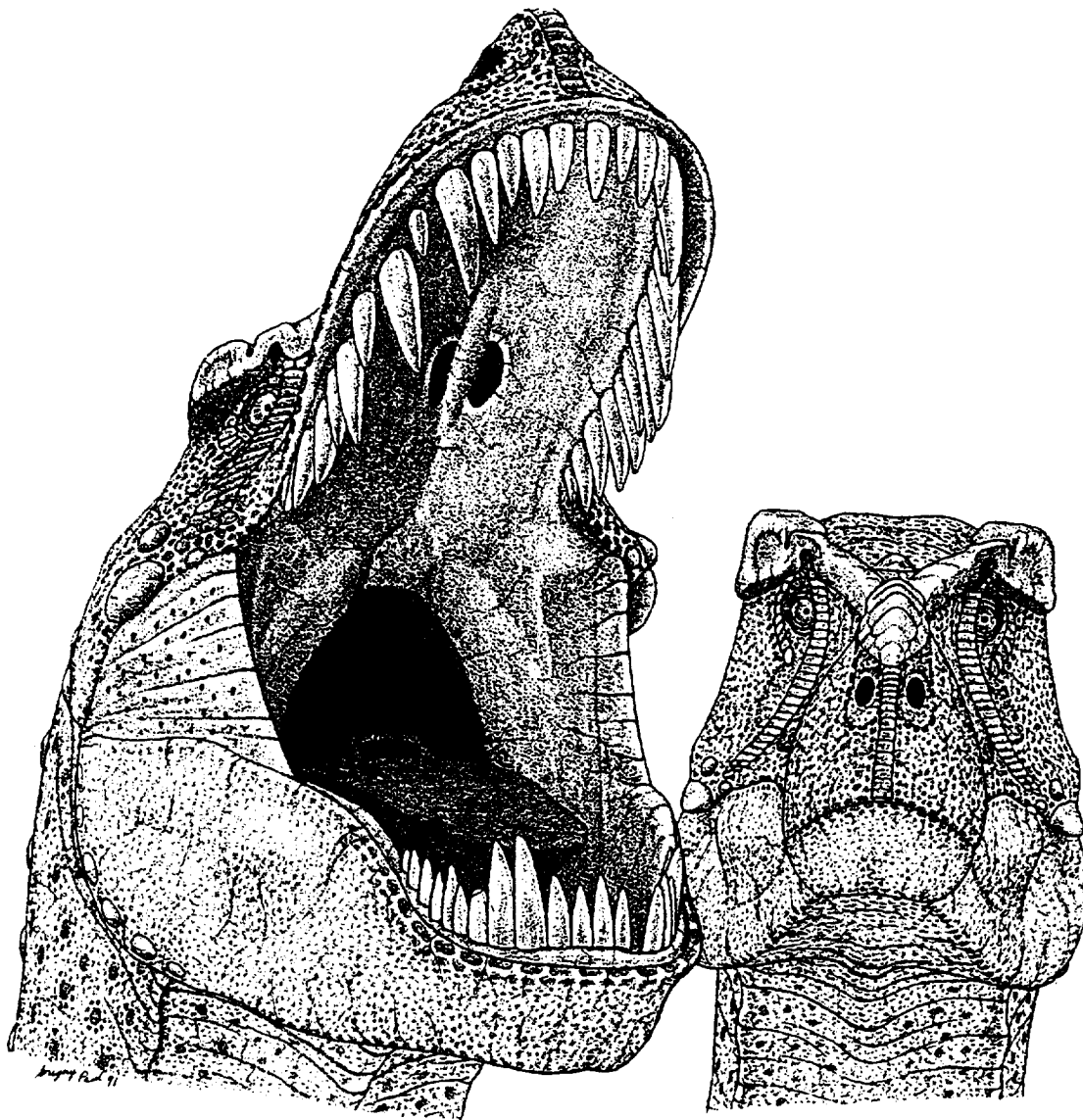Gary D. Rosenberg and Donald L. Wolberg

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Randall S. Spencer, Series Editor

GEOLOGY DEPARTMENT
INDIANA UNIVERSITY
PURDUE UNIVERSITY
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IUPUI

The Paleontological Society

Tyrannosaurus rex by Gregory S. Paul

The Origin and Evolution of Dino Fest

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History

Late in the summer of 1993, Robert Hall, Chairman of the Department of Geology, Indiana University-Purdue University at Indianapolis (IUPUI) thought it would be a good idea to invite a couple of dinosaur workers to campus to capitalize on the frenzy of enthusiasm for dinosaurs that the movie, *Jurassic Park*, had generated. However, what originally was to have been a couple of guest lectures quickly evolved into a three-day affair that was probably the first scientific conference--certainly the first paleontologic conference--for the general public, raising important issues about public involvement in science.

I first called Don Wolberg, Secretary of the Paleontological Society, who led a Geological Society of America field trip out of Santa Fe that I had been on. Don agreed to come and he offered to contact a couple of other vertebrate paleontologists as well. Don really meant "a couple of dozen" and, before I knew it, we had the makings of a conference. I also called Jim Farlow at the Department of Geosciences, Indiana University-Purdue University, Fort Wayne (IUPU-FW), who insisted that we not restrict our invitations to just a few of "the famous guys," because some of the lesser known vertebrate paleontologists had exciting things to say, too. Soon, we had the makings of a big, three-day conference whose participants included dinosaur hunters, paleopathologists, invertebrate paleontologists, Mesozoic paleoecologists, molecular biologists, commercial collectors, teachers, and artists. It was destined to attract a steady lecture audience of 400 throughout the three days of meetings, including young students and interested laypersons as well as professional researchers.

Amidst the expanding organization, Don called back to ask if we would like to display a few dinosaur bones during the conference. Again, Don left a word out. It soon became evident that he actually meant a "few truckloads" of fossils. Don had managed to charm some of the nation's most distinguished museums, as well as private, and commercial collectors and artists into loaning us dinosaur bones and other fossils and models including, but not limited to: a cast of a complete hadrosaur from China; a superbly mounted, never-before-displayed juvenile hadrosaur from the Hell Creek Formation of South Dakota; a whole bone bed loaded with dinosaur bones; a *Tyrannosaurus rex* skull and models; full scale models of *Ankylosaurus, Troodon, Coelophysis, Compsognathus*

and a juvenile *Protoceratops*; a working Dinamation model of *Deinonychus*; a sauropod ischium (holotype) and agatized femur; five kinds of dinosaur eggs; two original Charles Knight paintings of dinosaurs; a huge fern wall from Pennsylvania; ichthyosaurs; giant Cretaceous sardines (*Xiphactinus)* and mosasaurs (three dimensional casts freed from entombment in rock, as well as restorations of whole skeletons *in situ*); ten-foot-high palm fronds and fish from the Eocene of Wyoming; a large polished slab of a Precambrian banded iron formation (ancient algal mat) from Minnesota; replicas and actual samples of fossil crabs, dragon flies, shrimp, and pterosaurs preserved in the Jurassic Solnhofen limestone of Germany; a superb slab of Mississippian limestone with whole crinoids (calyx, stalks, and roots) from Indiana; Irish Elk antlers; bones of *Baptanodon*; a complete battery of Miocene shark teeth in a 6-foot-wide, life-sized reconstruction of a giant Miocene shark jaw from South Carolina; a breathtaking, huge collection of amber with entombed insects, tics, and spiders from Latin America; and a 20-foot-high reconstruction of a mastodon from Ohio-- all together enough to occupy almost three floors of the new university library, in beautifully illuminated space that seemed to be designed for just such purposes. (Edward Larabee Barnes, library architect, knows light.)

   Barbara Fischler, our head librarian enthusiastically took it all in stride. She even climbed scaffolding to help us put the head on the Chinese hadrosaur, the most significant dinosaur capitation since the proper heading of *Apatosaurus*. And Ann Koopman, the library liaison for the School of Science calmly helped us with logistics before, during, and after the three week exhibition. Mudge Morris, geology student and teaching assistant at IUPUI, inventoried and organized the exhibition with great care and effort. Several Geology faculty were especially helpful participants. Lenore Tedesco was always in the right place at the right time for long periods of time to do long, hard work. Lenore did more than could be expected of anyone throughout the entire meeting. Even after it was all over, she was right there to help crate and ship specimens or to transport people to and from the airport. Andy Barth prepared rock and mineral demonstrations for tours in the Department of Geology. Andy and Joe Pachut and their families, helped install and dismantle the displays in the library. Joe also reviewed several manuscripts for this volume.

   We thank Mike Triebold of Triebold Paleontology, Hal Halvorson of the Potomac Museum, Rick Hebden of Warfield Fossils, Bob and Sue Howell, Sherm Byers of Burning Tree Casting Company, Peter Larson and Joe Tippman of the Black Hills Institute, and Vito Bertucci for their dedication and hard work in installing and dismantling exhibits in addition to loaning us specimens. Additional specimens, casts, models, and posters were generously provided by The Carnegie Museum of Natural History, The Children's Museum of Indianapolis, DINAMATION, John Babiarz, the Engledow Company, John Fischner (Dream Star Productions), Susan Hendrickson, Hobbs Nursery, the Indianapolis Zoo, the Indiana State Museum of Natural History, the Los Angeles County Museum of Natural History, Glen Rockers (Paleo Search), and the Smithsonian Institution. Border's Bookstore kindly set up a display of paleontology books which was enthusiastically received by the public. During the conference, several private collectors and other exhibitors enthusiastically and generously brought in wonderful

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specimens to share with the public. With great regret, we have no record of their names, so that we cannot give them their proper due here.

Special thanks go to Karol Bartlett and Dallas Evans of the Indianapolis Children's Museum and Ron Richards of the Indiana State Museum of Natural History, who agreed at a moment's notice to loan us equipment, specimens, and curatorial expertise for the exhibits. Karol, Dallas, and Ron also participated in public presentations.

Chris Cumberworth of the Biology Department and Tim Brothers of Geography (both IUPUI) organized the "Mesozoic Forest" in the Biology greenhouse. Charles Turner (Orthopedic Surgery and Engineering), and Tom Katona (Dentistry) developed library demonstrations on bone histology and bone biomechanics. Mark Marshall, Department of Genetics, prepared a demonstration of DNA replication for the library and allowed us to CAT scan his fossil egg. Robert Holden and Ethan Braunstein (Radiology) granted access to the CAT scan facility in the IU School of Medicine and did the analyses.

The result was that, for three weeks, IUPUI boasted one of the best paleontology museums in the country. No doubt, Dino Bones ensured the success of the public outreach. Some 20,000 people came to campus specifically to see the exhibits during the conference, a total of 40,000 during its three-week stay. And more than 75,000 people were exposed to the displays if you also include patrons who came primarily to use the library's book collection. Many visitors to the Dino Bones exhibits were IUPUI students, staff, and faculty. Huge numbers were school kids and teachers from the Indianapolis Public Schools (IPS) and from schools in the surrounding communities, all of whom looked at exhibits, talked with collectors, watched artists, and listened to lectures. I shall especially remember one IPS teacher, Sarah Cowan, and her students who became fully involved in almost every moment of Dino Fest. Sarah went on to teach during the summer on an Indian reservation in Montana and took Indian children on dinosaur digs. I shall also warmly remember two visitors: the hunch-backed Chinese grandmother who smiled as she stretched to see the *Tsintaosaurus* and the little boy who stuck his head in the mouth of the *Tyrannosaurus rex* model and whispered, "Oh, wow, *dinosaur!*"

An important conference deserves an important dinner. So, Dino Feast was born. Diners ate fiddleheads of fern, seaweed in the form of sushi, a salad of exotic greens including flowers and oak leaves, chicken with pine nuts, and an iridium layer cake with Pleistocene icing-- and heard lectures from Karen Chin, Nick Hotton, John Ostrom, Claudia Barreto, and Ron Richards about what dinosaurs did and did not eat, dinosaur origins, the discovery of *Archaeopteryx*, the evolutionary link between dinosaurs and birds, and why dinosaurs are not found along the Wabash. Even the youngest children in the audience were riveted to their seats. Another measure of the Feast's success was the fact that tickets were being scalped for $250 just before the performance.

Big conferences require big funding. Fortunately, Bob Hall convinced David Stocum, Dean of the School of Science at IUPUI, to underwrite most of the conference cost. Gordon Fricke, Associate Dean of Sciences helped me find other, corporate sources of

funding. Indiana University and Purdue University sources, in addition to the School of Science at IUPUI, included the IU President's Council, Purdue University North Central, and the Dean of Faculty Development at IUPUI. We received additional external funding from the Geological Society of America (North Central Section), the alumni of the Geology Department, IUPUI, West Publishing, Wm. C. Brown Publishing, and Geraghty and Miller Corporation. Mayflower Movers helped transport the exhibits at their cost.

The Paleontological Society Council endorsed Dino Fest and agreed to help fund and to publish this proceedings volume.

Terry Forkner of Ameritech Corporation heard about the conference and quickly recognized its potential for public outreach of technology. In addition to a generous grant, Ameritech offered to broadcast a live, interactive session to the Indianapolis Public Schools (IPS) via their fiber optics network and with the assistance of Dorothy Crenshaw, Distance Learning Coordinator of the IPS. Then, NASA Lewis Research Center in Cleveland learned of our efforts, and offered to transmit the broadcast via satellite to schools across the continent to demonstrate the potential of teaching and learning via the "information superhighway." David Donaldson and Joetta Burrous and their crew at IUPUI's Integrated Technologies smoothed the way to and through the broadcast; Andy Sellers produced the show. We do know that thousands of students and teachers in schools in Montana, Idaho, Minnesota, Michigan, Ohio, New York, and Washington D.C. saw the broadcast. We can only guess at the total size of the audience.

We needed loads of volunteers, especially for tour guides. Angie Russo, geology undergraduate, took on the responsibility of finding and coordinating them, contacted public and private schools to schedule tours, arranged parking, and saw to a host of other issues. Larry Scusa, Geology Club President, was always available to help, and he rounded up other students on a moment's notice. Bob Barr, geology graduate student and library employee, quietly worked long hours with Ann Koopman at the library organizing the book display. Linda Horn, geology alumna, spent hours typing mailing labels for publicity which we sent around the country. Laurie Ireland helped uncrate, set up, take down, and crate fossils. Debbie Taylor, a teacher at Decatur Central High School kindly transcribed Jack Horner's lecture on *Tyrannosaurus rex* for this volume.

Judy Beaty, Beth Hemly, and Larry Studebaker coordinated the efforts of the Geology Department's alumni for the library welcoming reception.

Marc Frantz of the Department of Mathematics (IUPUI), Ray Mellen of New York, and Colin Whitfield of Cape Cod prepared art work for our program guide. Gary Schmitt in Medical Illustrations put in final order much of the art work for this volume.

Judy Martel at IUPUI's Media Relations did wonders getting Dino Fest into the newpapers and onto radio and TV programs. This required intense effort before, during, and after the conference. Thanks to her, IUPUI finally got some well-deserved attention. Diane Alfonso in Publication Services completed volumes of design work for tickets,

publicity brochures, and advertisements even though very little time was available for each job due to the short lead time of the conference. Harriet Rodenberg at University Place Conference Center, and Katie Hunter in Travel took care of hotel and travel arrangements.

One and only one person knew the entire administration of the conference inside and out. This burden was handled with great aplomb by Nancy Fribley, Secretary of the Department of Geology, who coordinated all of the administrative issues such as reconciliation of accounts, special requests for services directed to the physical plant, and participants' special needs. Nancy has a wonderful knack for anticipating problems and solving them without complaint. And she even found time to take dozens of photos of the Dino Bones exhibits for our archives.

Issues

As the conference unfolded, it became clear that Dino Fest touched upon important educational issues. They can all be lumped under the heading, "Public Involvement in Science." Interest in science has been waning for some time and the public's level of science literacy is rapidly declining. Fewer young men and women are studying for science careers in college, while increasing numbers are planning for more lucrative careers in business administration. Paleontology may well be the most popular of the sciences (it may be a little more difficult to get the crowds to come for a Chem Fest than we got for Dino Fest). Nevertheless, paleontology is hard-hit by the science malaise: paleontologists retiring from academia are not being replaced by young paleontologists; fossil collections in universities are being orphaned as a result and even discarded if foster museums cannot be found for them; pure research in paleontology is having a hard time getting funded (only 20 % of proposals submitted to the Paleontology/Stratigraphy Section of the National Science Foundation receive funding); paleontologists in the oil industry have become as scarce as a barrel of oil, and the few survivors of lay-offs and hiring freezes have formed the Industry Paleontology Managers Group to explore ways to improve the hiring of paleontologists; and even museums are laying off more and more personnel.

There are any number of reasons for such problems and we can only wonder about them here. The important point is that these problems prompt us to ask how we can communicate the continuing need for scientists and the ecstacy (as well as agony) of science to the general public?

Enter Dino Fest. Dino Fest was a success because the general public responded by attending in droves and because the general public participated in it. The general public sat in on lectures, heard scientists debate hot topics and discuss their recent break throughs. The general public brushed shoulders with scientists at the exhibits, talked to scientists, ate with them, and learned that scientists are people just like them. Dino Fest was also a success because it took place in Indianapolis, where there are few dinosaurs on display to satiate the public's appetite for them, and where such a diversity of

distinguished researchers, commercial collectors, and artists have never before assembled, and so were genuinely appreciated.

Rather than the last word in scientific conferences for the general public, Dino Fest is only the first. And there is much room for improvement. For example, even more student and teacher involvement in scientific presentations and interractions with researchers than took place at Dino Fest I would be desirable. The School of Science at IUPUI is already at work in this area. The School sponsors research mentorship programs which bring young scholars to campus to work with faculty in labs, especially during the summer. Moreover, the School has submitted proposals to foundations for funding a Science Learning Center. The proposals include plans for a new building, so that improving public involvement in science will be a permanent campus mission.

One thing is certain, public involvement in the fun of scientific discovery will lead to public understanding of science and public acceptance of it-- prerequisites for improving the condition of science. Everyone will benefit from the public's participation in science.

ACKNOWLEDGMENTS

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Dino Bones exhibit hall. Photo courtesy Nancy Fribley.

Giant Lizards:
A Brief History of Early Dinosaur Reconstruction

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INTRODUCTION

Although they have been extinct for more than 60 million years, dinosaurs are a familiar part of our culture. Featured regularly in entertainment, advertising and the news, they are recognized more readily in today's society than many living animals. Dinosaurs also function as a powerful educational tool, stimulating the interest of children and adults in the natural world. Moreover, they serve as a primary symbol of evolution, extinction and the long history of life on Earth. Yet, few people realize how radically our understanding of dinosaurs has changed since their discovery 170 years ago.

The initial recognition of dinosaurs as a distinct group of extinct animals was one of the major accomplishments of nineteenth century science. When first discovered, dinosaurs were an unexpected and almost alien life form whose interpretation was inhibited by a scarcity of good fossils and absence of close living relatives. For this reason, early nineteenth century dinosaur reconstructions, which were later ridiculed for their inaccuracies, may seem simplistic and conservative. In reality, they were quite innovative. Examination of this early work reveals just how profound these ideas actually were in light of the limited evidence available and demonstrates how interpretations changed as new fossil discoveries were made.

THE DINOSAUR FOSSIL RECORD

Contrary to public perception, scientifically useful dinosaur fossils are uncommon. Like many other large vertebrates, the majority of dinosaur fossils found are isolated bones, teeth and footprints that have limited research value. Reasonably complete dinosaur skeletons are extremely rare, and the first one was not collected until the 1860s. Of the 285 valid dinosaur genera known today, 45% are known from only a single specimen; merely 20% are based on essentially complete skulls and skeletons (Dodson, 1990). Furthermore, dinosaur fossils are not distributed uniformly in time or space. Although found on every continent, only a few places in the world yield relatively common and collectable dinosaur fossils. The best dinosaur-collecting sites are areas with little vegetation and extensive exposures of strata of the proper age such as the Gobi Desert and Alberta badlands. Here dinosaur fossils can be spotted as they are exposed by natural weathering processes. Other areas may also contain a large variety of dinosaurs but their discovery is hampered by a lack of exposures.

GIANT LIZARDS

Robert Plot, a clergyman, chemistry professor and first Keeper of the Ashmolean Museum at Oxford University, is credited with the earliest description of a probable

dinosaur fossil. In his book *The Natural History of Oxford-Shire* published in 1677, Plot described and figured part of a large femur that he believed to be a petrified bone. He certainly did not realize that this bone was of great age or from an extinct animal. Instead, he attributed the bone either to an elephant brought to England by the Romans or to a giant man (Delair and Sarjeant, 1975). Based on Plot's drawings, the bone is now thought to be from the dinosaur *Megalosaurus*, but, unfortunately, the specimen has been lost and this identification cannot be verified. Plot's identification may seem silly now, but at the time it was an important interpretation. The great age of the earth, the extinction of species or entire groups, and the theory of evolution had not yet been recognized. Instead, considerable debate focused on the nature of fossils—whether they were really petrified remains of animals and plants or the result of some unknown inorganic process.

By the end of the eighteenth century, the biologic origin of fossils was no longer in question and many were thought to be from animals and plants now extinct. Around this time, a number of authors mentioned or illustrated large individual bones from both Europe and North America, which they attributed to the fossils of whales or other large living animals (Delair and Sarjeant, 1975). Some may actually have been of dinosaur origin, however. In 1808, the great French anatomist Baron Georges Cuvier published a description and illustration of some fossil bones from the Jurassic rocks of France. Although Cuvier believed that these bones belonged to fossil crocodiles, at least some of the specimens belonged to a carnivorous dinosaur (Michard, 1992).

William Buckland, the first professor of geology at Oxford University and one of the most influential individuals in the new sciences of paleontology and geology, was the first to recognize that dinosaurs were unique land-dwelling fossil reptiles (Delair and Sarjeant, 1975). Buckland travelled widely throughout Great Britain and the continent, collecting fossils, studying geology, and acquiring live animals for the large menagerie he kept in his home, all of which made him an extremely popular lecturer (Colbert, 1968). Among Buckland's many accomplishments was the recognition, in 1829, that coprolites were fossil feces, which could provide important information on the eating habits of ancient animals (Rupke, 1983). Around 1818, he acquired some fossil bones and teeth from the Jurassic rocks near Oxford. Although having only a small part of the skeleton, Buckland deduced that they belonged to a large, land-dwelling, carnivorous reptile, which he later named *Megalosaurus* (Buckland, 1824). *Megalosaurus*, which means "giant lizard" was the first valid scientific name given to a dinosaur.

Around the same time that Buckland was working on *Megalosaurus*, another Englishman, Gideon Mantell, was acquiring and studying similar fossils. A physician by training, Mantell was a gentleman naturalist. Unlike Cuvier and Buckland, who were both employed as professional paleontologists, Mantell was never employed by a scientific institution such as a university or museum, and many of his paleontologic endeavors were self-financed. Throughout the nineteenth century, gentleman naturalists were responsible for collecting many of the fossils that were used scientifically. Some of them became scientists in their own right by describing many of the fossils they collected and studied, and a few, like Mantell, could be counted among the most prominent scientists of their day.

Mantell made extensive collections of fossils in southern England, which he described in several books on the geology of the area. Around 1821 at Tilgate Forest, he and his wife Mary found a number of unusual fossil teeth that were clearly from a large herbivorous animal (Dean, 1990). Mantell showed these teeth to many of his fellow scientists, including Cuvier, but no one recognized their "reptilian" nature (Edmonds, 1979). Eventually, Mantell was able to demonstrate that these fossil teeth were very similar
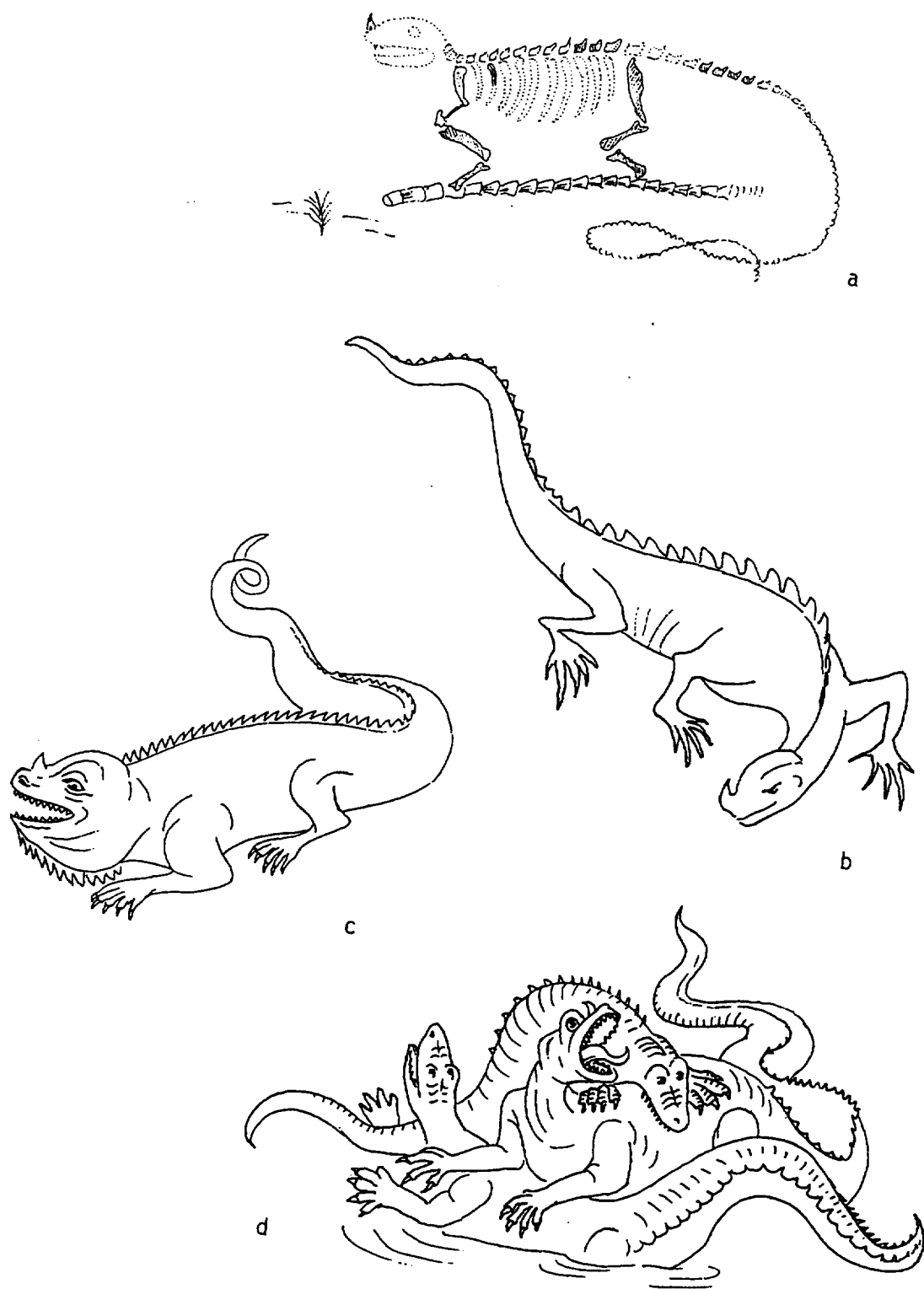
Figure 1. The earliest dinosaur reconstructions: a) *Iguanodon,* Mantell, c.1835; b) *Iguanodon,* Fisher *in* Buckland, 1836; c) *Iguanodon,* George Nibbs, c. 1838; d) *Iguanodon* and *Megalosaurus,* John Martin, c. 1838. Figures 1-5 were drawn by Joanne Kluessendorf.

to the much smaller teeth of the living *Iguana* lizard and, in 1825, Mantell named his fossil *Iguanodon,* meaning "iguana tooth." The careers of both Buckland and Mantell were enhanced because Cuvier concurred that their finds were from previously unknown large fossil reptiles (Norman, 1991). Additional work enabled Mantell to publish a paper in 1831 on "The Geological Age of Reptiles" in which he stated that there was a time before the age of mammals when *"...the earth was peopled by oviparous quadrupeds of a most appalling magnitude, and that reptiles were the Lords of the Creation..."* Although the prominence of marine reptiles during that ancient era had been recognized previously, Mantell demonstrated that the land was also dominated by reptiles such as *Megalosaurus* and *Iguanodon,* describing for the first time what is now known as the "Age of Dinosaurs."

Although the large size and reptilian nature of both *Megalosaurus* and *Iguanodon* were recognized, neither Buckland nor Mantell attempted to reconstruct these animals based on the few scattered bones and teeth they had available at the time of their original descriptions. The first opportunity for a reconstruction came about in 1834 when Mantell acquired the newly-discovered Maidstone *Iguanodon* specimen. Although disarticulated, this specimen, which comprised about one-third of a single skeleton (Swinton, 1951), was the first partial dinosaur skeleton ever unearthed and studied. The Maidstone specimen provided important information about relative size and some specific characteristics of *Iguanodon,* but important parts of the animal were still unknown. This, coupled with the lack of a large terrestrial reptile for comparison, gave Mantell significant problems in his attempt at reconstructing the *Iguanodon* skeleton. His unpublished sketch (Fig. 1a) shows that his solution to these problems was simply to depict the *Iguanodon* skeleton as that of an enormous lizard-like reptile—a reasonable interpretation based on the available evidence. An interesting aspect of Mantell's reconstruction is his placement of a spike-like bone on the animal's nose, which is now known to be an error. At first glance, this may seem to be an unusual location for this peculiar bone, but undoubtedly Mantell got the idea from the horn-like projection that some modern species of *Iguana* have in the exact same position.

Interestingly, it was Buckland who published the earliest reconstruction of a dinosaur in the flesh when, in 1836, he included a small sketch of *Iguanodon* by Joseph Fisher on a stratigraphic chart of the Earth's crust. This illustration (Fig. 1b) shows a very lizard-like animal probably based on Mantell's reconstruction, including the placement of the "horn." In 1838, a similar, but more elaborate illustration (Fig. 1c), was included as a frontispiece in a book of poetry by George Richardson, who had been the curator for Mantell's private museum (Torrens and Cooper, 1985). This illustration was drawn by George Nibbs, probably under Richardson's or Mantell's direction. Also in 1838 and probably under Mantell's direction, a frontispiece illustration for his book *Wonders of Geology* was created by John Martin, a famous painter of historical events in the Romantic tradition (Rudwick, 1992). This dramatic scene depicted a similar-looking *Iguanodon* locked in mortal combat with an equally lizard-like *Megalosaurus* (Fig. 1d). These two illustrations are the first attempts to reconstruct dinosaurs as living animals within their natural habitat.

TERRIBLE LIZARDS

The lizard-like reconstructions of *Iguanodon* and *Megalosaurus* remained in vogue until the 1850s. By the early 1840s, however, additional discoveries of *Iguanodon* and *Megalosaurus* specimens had been made, and a new dinosaur, *Hylaeosaurus,* had been found by Mantell. Richard Owen, an outstanding comparative anatomist who would later
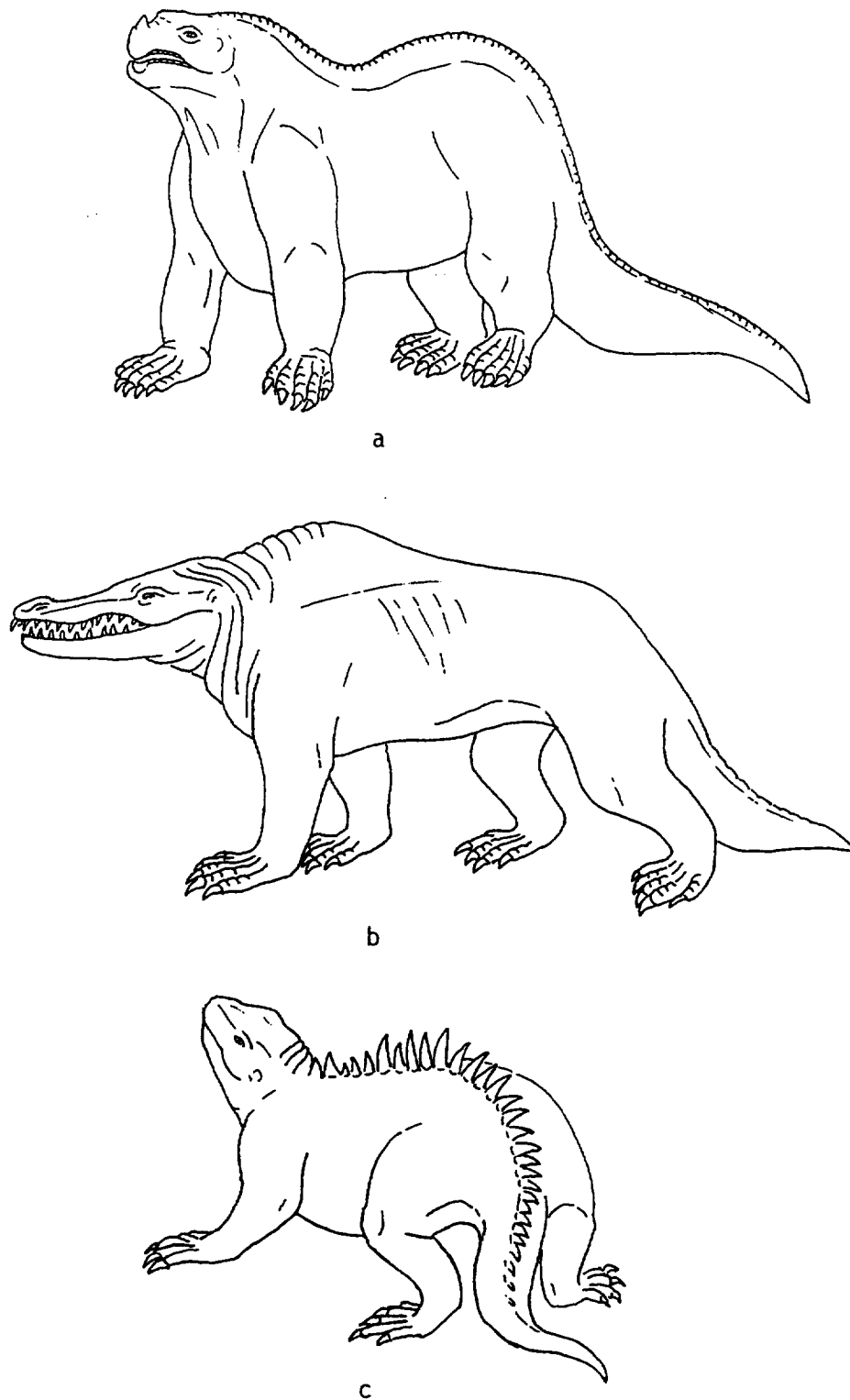
Figure 2. The Crystal Palace dinosaurs. a) *Iguanodon;* b) *Megalosaurus;* c) *Hylaeosaurus,* modified from *Waterhouse Hawkins Diagrams of the Extinct Animals,* a series of posters marketed in the 1860s (Rudwick, 1992). These illustrations were based on the life-size models that Hawkins and Owen created for the Crystal Palace grounds in 1854.

become known as the "English Cuvier," examined all of this material in a comprehensive study of British fossil reptiles. He was, for the first time, able to recognize that these three animals represented a distinct group of ancient terrestrial reptiles. Owen proposed the name "Dinosauria" ("terrible lizards") for these animals at the 1841 meeting of the British Association for the Advancement of Science (Owen, 1842). He concluded that dinosaurs displayed a number of unique characteristics, and that they were more like large land mammals than huge lizards in their general proportions and posture. Owen was famous for his ability to reconstruct fossil vertebrates based on limited material, such as his amazing prediction of the existence of large flightless fossil birds (moas) in New Zealand based on a single bone fragment. Therefore, the meager material available for these three dinosaur species did not dissuade him from proposing new reconstructions dramatically different from those of Mantell and Buckland.

An outstanding opportunity to create new dinosaur reconstructions presented itself in 1852 when plans were made to create life-size prehistoric animal sculptures for the grounds of the Crystal Palace near London (Desmond, 1976). The artist Benjamin Waterhouse Hawkins was contracted to construct these animals under Owen's direction. This unprecedented exhibit, which opened in 1854 (Norman, 1991), immediately captured the public's imagination and marked the introduction of dinosaurs into popular culture. Life-size models of the three best-known dinosaur species at the time, *Iguanodon, Megalosaurus* and *Hylaeosaurus,* were created (Fig. 2a-c). In a radical departure from earlier reconstructions, Owen and Hawkins lifted dinosaurs out of their lizard-like sprawl and off their bellies into an upright posture supported by four pillar-like legs. This innovative view of dinosaurs represented a major advancement in our understanding of these animals. Although specific aspects of the reconstructions were later proven inaccurate based on new fossil discoveries, and his ideas would fall out favor for many years, Owen's concept of dinosaurs as active terrestrial creatures would regain acceptance in the twentieth century.

One error that Owen made, however, led to the continued misinterpretation of critical evidence that would have radically changed his reconstructions. Owen believed, with very little evidence, that *Megalosaurus* and *Iguanodon* had mammalian-like feet with five toes each. Since 1800, large three-toed fossil footprints of bipedal animals had been known from Triassic rocks of New England, and were long thought to have been made by giant extinct birds (Hitchcock, 1858; Steinbock, 1989). It is now recognized that these are the tracks of bipedal dinosaurs. If Owen had not been biased in his assumption about the number of toes on *Iguanodon* and *Megalosaurus,* he may have been able to identify these tracks as belonging to dinosaurs, allowing him to deduce that at least some of them were bipedal.

LEAPING LIZARDS

A few years after the Hawkins-Owen Crystal Palace models were completed, a discovery in North America was to dramatically alter the appearance of dinosaur reconstructions. In 1858, William Foulke recovered a large part of a disarticulated dinosaur skeleton from Cretaceous rocks at Haddonfield, New Jersey. Joseph Leidy, the founder of American vertebrate paleontology, named this dinosaur *Hadrosaurus,* and made the important observation that its hind legs were much longer than its front legs. This led him to conclude that *Hadrosaurus* may have browsed in a kangaroo-like erect position, supporting itself on its hind legs and tail (Leidy, 1858). This is the first time that any dinosaurs were interpreted to have been at least occasionally bipedal.

Figure 3. The first bipedal reconstructions. a) *Hadrosaurus*, modified from Hawkins' painting of the prehistoric animals from the Cretaceous of New Jersey (c. 1870) in the series at Princeton University; b) *Laelaps*, modified from Cope (1870); c) standard pose for *Iguanodon* based on Dollo's work in the 1880s, modified from Neave Parker (c. 1950s).

This idea was reinforced in 1866, when Edward Drinker Cope described *Laelaps,* a carnivorous dinosaur also from Cretaceous rocks of New Jersey. Cope, who had been a child prodigy capable of making detailed anatomical notes on ichthyosaur fossils as a young boy (Colbert, 1968), would become one of the most prominent nineteenth century paleontologists, publishing more than 1400 papers on both fossil and living vertebrates over his career. Although incomplete, the skeleton of *Laelaps* exhibited an even greater disproportion between its fore- and hind-limbs than Leidy had observed in *Hadrosaurus.* Because the only living bipedal animal with a long tail like these dinosaurs is the kangaroo, Cope speculated that *Laelaps* may also have hopped or leaped as its primary means of locomotion.

In 1861, the first complete dinosaur skeleton found anywhere in the world was recovered from the famous Jurassic Solnhofen fossil beds of Germany. Surprisingly, this dinosaur, *Compsognathus,* was minute (only about 3 feet long) compared to those previously described. Both Cope and the English biologist Thomas Huxley recognized the bird-like affinities of this animal (Desmond, 1976). Despite the completeness of this fossil, it played a very small role in the reconstruction of other dinosaurs.

In the late 1860s, the Board of Commissioners of Central Park in New York took note of the huge success of the Hawkins-Owen Crystal Palace prehistoric animal models. The Board decided to construct a similar indoor display of North American prehistoric animals, which would include *Hadrosaurus* and *Laelaps* (Colbert and Beneker, 1959; Desmond, 1974). Benjamin Waterhouse Hawkins was hired to construct these models also and, in 1868, he began a series of life-size reconstructions based on Leidy's and Cope's new interpretations. After several years' work, both a skeleton and life model of *Hadrosaurus* were constructed, but, unfortunately, the museum was never finished. The infamous Boss Tweed Ring, who had gained control of the Park Commission, had no interest in spending money on the models or museum. Angered by Hawkins' criticism for their lack of financial support, in 1870, the Tweed Ring had all of his completed models smashed and buried in the park. Apparently Hawkins did save the molds for the *Hadrosaurus* skeleton, and copies were exhibited in a number of museums well into the 1920s, although none survive today (Ryder, 1986).

Following the demise of the Central Park museum, Hawkins produced a series of paintings depicting prehistoric life for Princeton University. In these paintings, Hawkins portrays *Hadrosaurus* and *Laelaps* as erect, active bipeds (Fig. 3a), but, interestingly, he depicts *Megalosaurus* as a quadruped even though he shows the proper disproportion between its fore- and hind-limbs. In 1870, Cope published a reconstruction of *Laelaps,* showing it in a kangaroo-like pose (Fig. 3b).

In 1878, Belgium became one of the most famous dinosaur localities in the world after coal miners at the village of Bernissart encountered fossil bones when digging a new mine tunnel about 1000 feet below the ground surface. Over the next several years, Louis De Pauw from the Musée Royale d'Histoire Naturelle supervised the excavation of more than thirty skeletons of *Iguanodon,* most of which were articulated and many of which were complete (Norman, 1987). For the first time, the entire skeleton of a dinosaur species was known from, not just one, but from a population of animals as a result of this unprecedented collection. Over the next forty years, Louis Dollo, also of the Musée Royale d'Histoire Naturelle, studied this enormous amount of material, turning out a series of papers on *Iguanodon.*
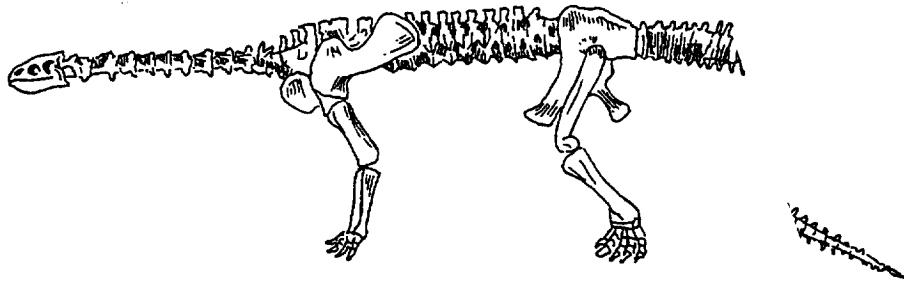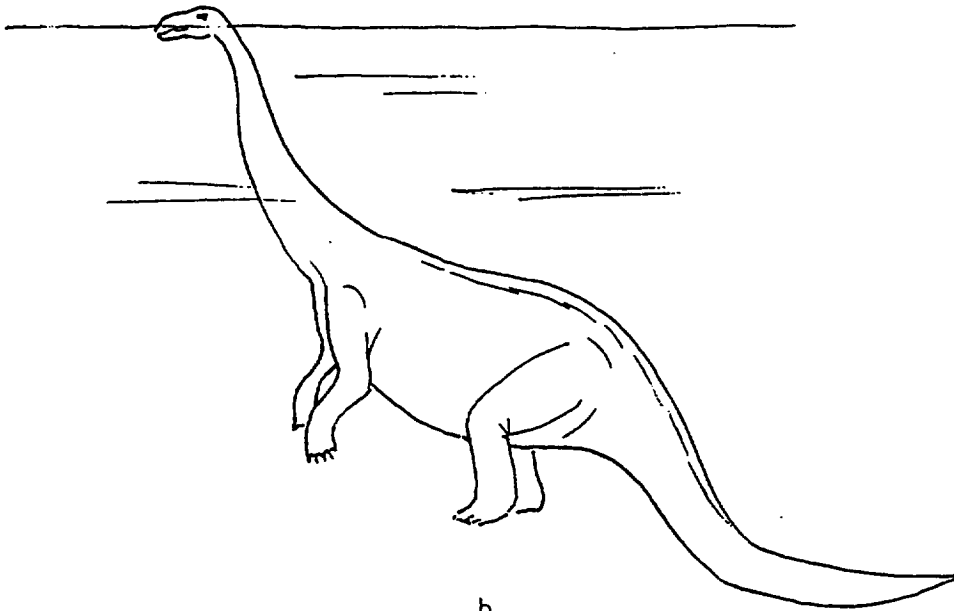
Figure 4. Early sauropod reconstructions. a) *Camarasaurus* by Ryder (c. 1878) under Cope's direction, modified from Mook (1914); b) *Amphicoelias* in aquatic lifestyle as depicted by Knight (c. 1897) under Cope's direction, modified from Desmond (1976).

Many of the questions and mistakes resulting from the earlier work by Mantell and Owen were soon resolved. The "horn" that Mantell had placed on *Iguanodon's* nose was discovered to be a unique "thumb" spike. The animal was clearly bipedal, and its three-toed hind feet unmistakably matched fossil footprints found in rocks of the same age. Despite this vast amount of excellent material, important features, especially the posture of *Iguanodon*, remained in question. The complete specimens only emphasized the differences between dinosaurs and all living animals, which thus made it more difficult to justify their use as analogues. For example, although the thumb spike is now properly located, it's exact function remains speculative as no living animal has a similar feature. When time came to mount the first Belgian *Iguanodon* fossils, skeletons of a kangaroo and a flightless bird were used as guides. Unfortunately, neither animal was perfect for this purpose as the bird has no tail, its legs are fully extended, and its body is tilted forward, whereas the kangaroo has a tail but its legs are flexed for hopping, and its body is erect. As a result, the active leaping stance suggested by Cope for *Laelaps* was abandoned, and *Iguanodon* was presented in a plodding upright, tail dragging posture (Fig. 3c). This was the first use of this now-familiar pose, which would become the standard for bipedal dinosaur reconstructions until the 1960s.

THUNDER LIZARDS

About the same time as the Belgian *Iguanodon* find, a vast new area rich in dinosaur fossils was discovered in the American West. For the first time, an almost inexhaustible supply of dinosaur fossils became available for scientific research. In just a few short years, more dinosaur fossils were collected here than were found in the entire preceding century throughout the world. These new discoveries were made primarily by Othniel Marsh, professor of paleontology at Yale University and a nephew of millionaire George Peabody, and Edward Cope, both of whom had private funding sources for their scientific pursuits. Although their efforts began amicably, their relationship deteriorated rapidly into mutual hatred, culminating in one of the most infamous scientific feuds in history (Colbert, 1968). Anxious to achieve priority in naming new species, their quest for specimens drove both Marsh and Cope into investing huge sums of money on the collection and study of fossil vertebrates.

One positive result of their competition was the discovery and study of the famous Jurassic Morrison Formation, where new types of dinosaurs and better specimens of previously known dinosaur groups were uncovered. Morrison dinosaurs are seldom found articulated and complete like the Belgian *Iguanodon* specimens, but individual bones and partial skeletons are common. Among the most important discoveries made by Cope and Marsh were the first reasonably complete specimens of sauropods, the gigantic long-necked, long-tailed dinosaurs, which have come to symbolize dinosaurs in general. Interestingly, sauropod bones had been known to Buckland, Mantell and Owen, all of whom had collected or studied material of the English Jurassic sauropod *Cetiosaurus*. The *Cetiosaurus* material, which amounted to only a few bones, however, was initially thought to be from a huge whale- or crocodile-like aquatic reptile, not a dinosaur (Owen, 1842). The Morrison dinosaurs, although of different species, made it possible to quickly establish the general sauropod body form and, in 1878, John Ryder, under the direction of Cope, produced the first sauropod reconstruction—a life-size drawing of a *Camarasaurus* skeleton (Osborne, 1906; Mook, 1914) (Fig. 4a).

Not recognizing Cope's priority in naming *Camarasaurus*, Marsh named different specimens of the same animal *Morosaurus*, which literally means "stupid lizard" (Norman,
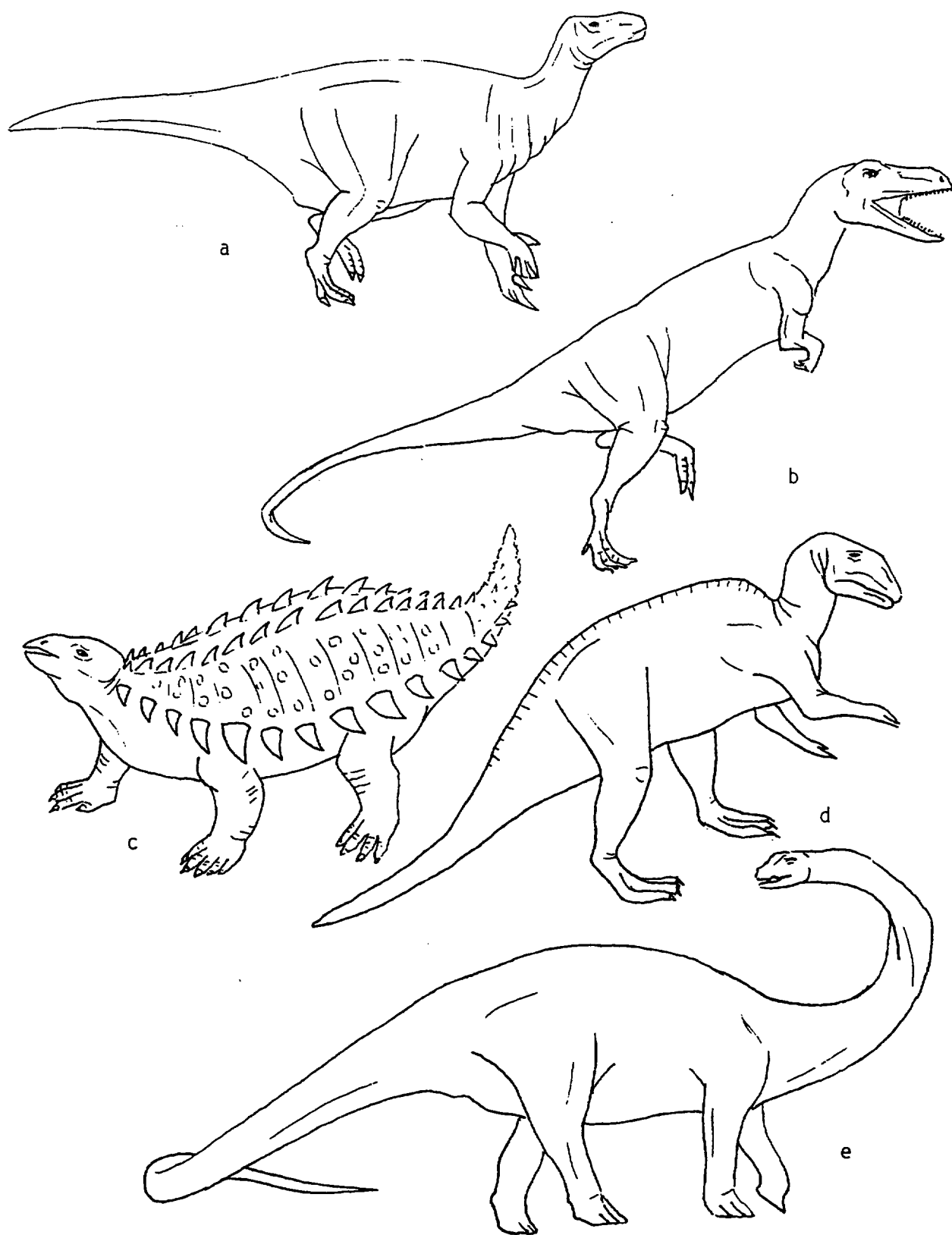
Figure 5. Modern reconstructions. a) *Iguanodon* modified from Lambert (1989); b) *Megalosaurus* modified from Lambert (1989; c) *Hylaeosaurus,* modified from Jenny Halstead *in* Baldwin and Halstead (1991); d) *Hadrosaurus,* modified from Lambert (1989); e) *Cetiosaurus,* modified from Lambert (1989).

1991). A few years later, when describing another new sauropod (the "thunder lizard" *Brontosaurus,* now known as *Apatosaurus*), Marsh followed the same theme, commenting that its extremely small head indicated a stupid, slow-moving reptile which, because of its huge body size, was probably amphibious (Desmond, 1976). As the gigantic size of sauropods became widely recognized, a great debate on their general posture and behavior ensued, and it became generally accepted that these dinosaurs supported their great weight by spending all or most of their time in water with their long necks functioning as snorkels (Desmond, 1976) (Fig. 4b). A combination of Louis Dollo's plodding bipedal dinosaurs and Marsh's ideas of sluggish, dim-witted, reptilian sauropods became the predominant models for all dinosaur reconstructions, influencing our view of these animals for the next 80 years.

NO MORE LIZARDS

Throughout the first half of the twentieth century this general view of dinosaurs prevailed with surprisingly little change despite numerous new discoveries and a vast amount of research on dinosaurs in general. Indeed, this style of dinosaur reconstruction became highly popularized through the art of Charles R. Knight (Czerkas & Glut, 1982), the most famous portrayer of prehistoric animals since Hawkins.

The lack of change in dinosaur reconstructions over this long period reflects the recurring problem posed by the absence of modern analogues. Even though many dinosaurs were now known from reasonably complete skeletons, their physiology and function were still poorly understood, impeding changes in the accepted views of their behavior and appearance. The major stumbling block was the reptilian ancestry of dinosaurs, which caused paleontologists to force them into the behavioral and functional molds of modern reptiles, ignoring the fact that dinosaurs filled ecological roles in the Mesozoic world that are now occupied primarily by terrestrial mammals. A growing awareness of these factors over the last thirty years has brought about the revitalization of dinosaurs in the minds of both scientists and the general public. The reptilian mold has been broken. We now know that dinosaurs are unique animals in their own right, and that they should not be modelled in the image of any other animal group. These new ideas have allowed more accurate, dynamic, and lifelike reconstructions of dinosaurs than ever before possible (Fig. 5a-e).

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What the Fossil Record of Dinosaurs Tells Us

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INTRODUCTION

Dinosaurs were enormously successful animals. They inhabited all seven continents, including polar regions during the Mesozoic. Their temporal range, as currently understood, extends from the Carnian stage of the Late Triassic beginning 228 Ma, to the Maastrichtian stage of the Late Cretaceous, ending 65 Ma. With a temporal span of 163 million years, dinosaurs cannot be judged as failures by puny naked bipeds who have been here for two million years or less and who threaten not only their own existence but that of much of the biosphere. The fossil record of dinosaurs is a complex document that cannot merely be read at face value but which must be carefully evaluated with respect to its inherent biases. There is much we wish to ask about dinosaurs that can only be answered with a mature reliable record. The object of this essay is to discuss some of the factors that impact both on dinosaur diversity itself, and on our understanding of that diversity. While fossils have an objective existence in the rocks, our understanding of their record is the result of a very human process of scientific discovery, subject to the contingencies and biases of history (Dodson, and Dawson, 1991).

DINOSAUR SCIENCE AS A HUMAN ACTIVITY

The fossil record is not a given fact, literally a datum, but may rather be viewed as a work in progress. New dinosaurs are being added at the rate of about six per year, a rate that has prevailed since 1970. A critical evaluation of dinosaur genera (Dodson, 1990a; Weishampel et al., 1990) recognized 285 genera as of 1988. Since then, the number has grown by 30 or more. When Richard Owen coined the name Dinosauria in 1842, only 7 legitimate genera had been named. When H.G. Seeley recognized the division of the Dinosauria into the Saurischia and the Ornithischia in 1887, only 37 genera that we currently recognize had been described (Seeley himself set somewhat of a dubious record, having named 22 genera of dinosaurs based primarily on dubious, scrappy and indeterminate material, of which only the
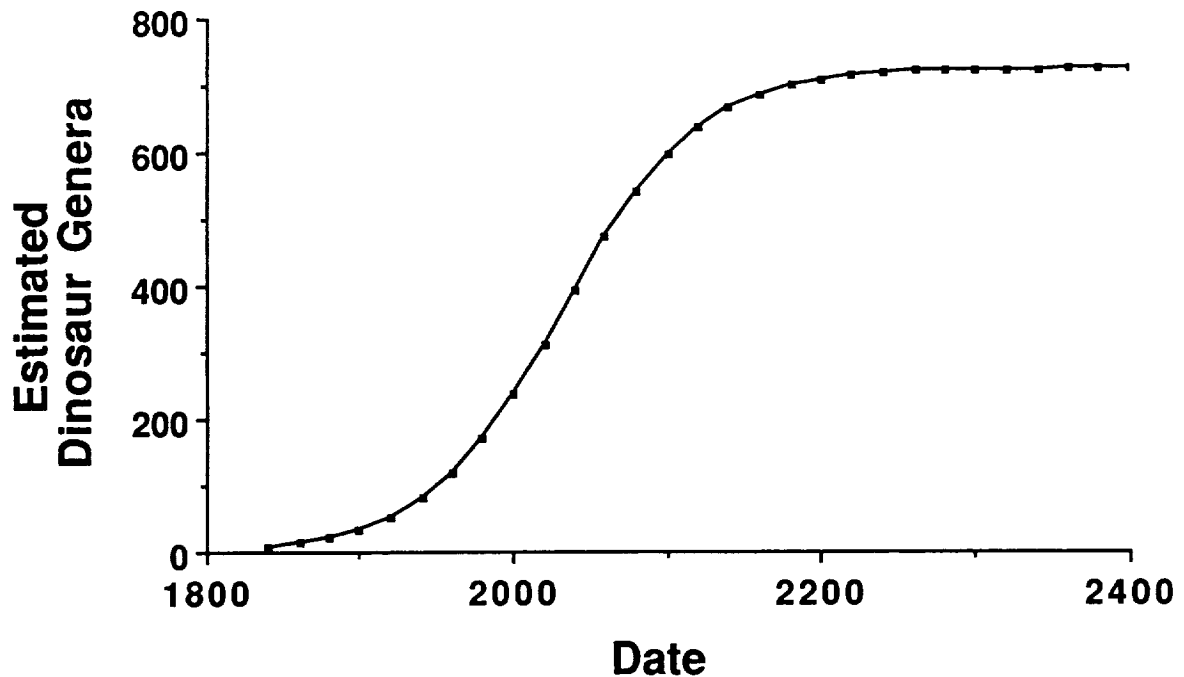
FIGURE 1--The rate of accumulation of new dinosaur genera extrapolated from the past into the future. This logistic curve suggests that paleontological sampling may be complete in 200 years, when 725 genera of dinosaurs have been described.

sauropod, *Agrosaurus*, remains). As of 1969, 170 valid genera of dinosaurs had been named. Since then, the number of valid dinosaur genera has increased by approximately 85%. Dinosaurs entering the lexicon in 1993 include *Eoraptor, Utahraptor, Mononykus, Shuvosaurus, Anasazisaurus* and *Naashoibitosaurus*. It is further striking that national biases are evident. The dinosaur was born in England in 1824, and dinosaur science remained predominately an Anglo-American enterprise for more than a century. Of the 13 most prolific dinosaur scientists between 1824 and 1969, 10 were British, American or Canadian, and all were male. In the period since 1970, the list of seven most productive dinosaur scientists (that is, those who have described the greatest numbers of new genera) includes two women and but a single English-speaker (Dodson and Dawson, 1991).

It would be pedestrian to predict that our knowledge of dinosaurs will continue to grow. In fact it will grow at an asymptotic rate for another century or two (Figure 1). Dinosaur genera doubled in 30 years between 1877 and 1907 from 32 to 64 genera, and doubled again in another 30 years, 1907 to 1937, reaching 128. The latest doubling, from 128 to 256, required 46 years (but it took only 38 years to go

from 143 to the current 285). Even if the next doubling to 512 genera requires 60 years, it will still be accomplished before the middle of the next century. There is absolutely no indication that the fossil record of dinosaurs will be depleted any time soon.

In order for this record to be useful it must be viewed critically. For example, the theropod *Megalosaurus* Buckland, 1824 has been claimed for remains ranging in age from Late Triassic to Late Cretaceous, thus essentially for the entire age of dinosaurs. Yet it is estimated that the duration of an average genus of dinosaur ranged from 5 to 7.7 million years (Dodson, 1990a). It is proper to be skeptical of claims of *Megalosaurus* from all over the world for all of the Mesozoic. It is helpful to recollect that the type of *Megalosaurus*, *M. bucklandi*, comes from the Stonesfield Slate of Oxfordshire, England, of Bathonian age (Middle Jurassic), approximately 166 to 161 Ma. The type specimen consists only of a partial dentary. As no further cranial or postcranial elements are associated with the type, it is very difficult to refer further finds to it, even in England. The history of the taxon is such that when genuinely diagnostic fossils are found, they generally become genotypes of new taxa, some having first been described as species of *Megalosaurus* (e.g., *Metriacanthosaurus, Proceratosaurus, Majungasaurus, Dilophosaurus*). Other Middle Jurassic theropods from England and Europe have been described as separate genera from the start (e.g., *Eustreptospondylus, Piveteausaurus*). All told, 30 species of *Megalosaurus* have been named. Of these, 12 have been referred to other genera. Most of the rest are based on such dubious material that they enjoy no claim to validity. This is not a pretty story but because it is so instructive it must be told. *Megalosaurus* is the oldest dinosaur that received scientific validation. The second oldest, *Iguanodon* Mantell, 1825 has fared somewhat better because, even though the type specimen consisted only of three teeth from Sussex, England, numerous skeletons have come to light subsequently in England, Belgium and Germany. Nonetheless, 17 species have been referred to *Iguanodon*, the majority of these without value (Norman and Weishampel, 1990). Two valid species are of significant interest, *I. orientalis* from Mongolia and *I. lakotaensis* from the United States (South Dakota) because of their geographic separation from the type area.

The question may be raised as to what is a dinosaur species? It may be a source of puzzlement to children why only a single dinosaur has a species name, the infamous *Tyrannosaurus rex*. This binomial (which means "two names") is so well known both because it is intrinsically an excellent evocative and pithy composition ("tyrant lizard

king") and because of the public relations skills of its namer, Henry Fairfield Osborn. Every genus has a species, the name usually being honorific, geographical or descriptive. It is inconsistent and somewhat objectionable that only *Tyrannosaurus* is accorded its full name in popular accounts. Following for a moment the line of thought that every species has a genus, every genus a family, every family an order, every order a class, and every class a phylum and kingdom; each of these may be called a taxon (plural taxa). In this example, *Tyrannosaurus rex*, is in the family Tyrannosauridae, order Saurischia, class Reptilia, phylum Chordata, kingdom Animalia. A species name by itself has no meaning. There may be hundreds of species named "rex", including the ornithopod dinosaur *Othnielia rex*, but there is only one *Tyrannosaurus rex*. Each taxon may have only one name, and the first one has priority over all others. A famous example is *Apatosaurus* Marsh, 1877 which has priority over *Brontosaurus* Marsh, 1879.

But the more important problem is how species are defined for dinosaurs. A priori taxonomic philosophies of lumping or splitting are germane in this context. Older practices of naming each specimen as new (extreme splitting) have in general given way to population-variation concepts that recognize biological variability as an expectation rather than as an exception. This is especially appropriate for dinosaurs because growth series are well known, and variation due to sexual dimorphism and in display structures is also documented (e.g., Dodson, 1975 on *Corythosaurus* and *Lambeosaurus*; Dodson, 1976 on *Protoceratops*; Ostrom and Wellnhofer, 1986 on *Triceratops*; Lehman, 1989 on *Chasmosaurus*; Dodson, 1990b on *Centrosaurus* and *Monoclonius*; Forster, 1990 on *Tenontosaurus*). Many of these studies either lump previously described species or genera into a smaller number of species or a single one. In other cases, however, notably for *Protoceratops* and *Tenontosaurus*, only a single species was recognized from the start despite a wide size range of individuals. A common feature of all of these studies, is that multiple specimens are available for analysis. This highly desirable circumstance is met somewhat infrequently. Nearly half (45%) of all dinosaur genera are represented by only a single specimen (Dodson, 1990a), and for these taxa no variation is in principle possible.

As a general biological principle, diversity, that is, the number of genera or species, decreases with increasing body size. Thus the number of species per genus may be expected to decline with increasing body size. This phenomenon is well illustrated with living mammals. For instance, Macdonald (1984) recognizes 28 species in the genus *Felis* (small cats), ranging in size from 2 kg to 103 kg, but most less than 20 kg. There are only 5 species in

the genus *Panthera* (large cats), and these range from 100 to 384 kg in weight. This pattern is repeated in herbivores. For instance, there are 16 species of *Cephalophus* (duikers), ranging from 6 to 80 kg, but mostly less than 20 kg; 8 species of *Cervus* (deer) ranging from 50 to 450 kg; 5 species of *Bos* (cattle) from 350 to 900 kg; two strictly allopatric species of *Rhinoceros*, one being Indian, the other Javan, 1400 to 2200 kg,; and one *Elephas*, 5000 kg. Dodson (1990a) estimated 1.2 species per genus of dinosaur. Although this figure may seem low, it seems consistent with the generally large body size of dinosaurs, particularly herbivores. Most dinosaurs, as presently understood, have only a single species per genus. One dinosaur that seems genuinely speciose is *Psittacosaurus,* with four valid species (Sereno, 1990). This is a conspicuously small dinosaur, 2 m. in length and less than 50 kg in weight. But in practice, because dinosaur species are usually difficult to define and recognize, the genus is a useful working level for dinosaur paleontology.

Unlike mammals, dinosaurs lacked permanent, non-growing teeth and consequently tooth morphology does not prove to be very reliable for dinosaur taxonomy below the taxonomic level of family. Dinosaur paleontology should not succumb to mammal-envy. More than 40 dubious genera of dinosaurs are based on teeth alone. The first American dinosaurs are *Deinodon, Trachodon, Paleoscincus* and *Troodon*, all named by Leidy in 1856. But who can say what these animals looked like? All but *Troodon* are on the scrapheap of paleontological history. *Troodon* forms a particularly instructive case history. It has variously been considered a lizard, a pachycephalosaur, a carnivorous ornithischian, and finally a maniraptoran theropod. Conversely, the names *Stenonychosaurus, Polyodontosaurus* and *Pectinodon* have all been subsumed within *Troodon* (Currie, 1987; Currie, et al., 1990). The habit of naming dinosaurs on the basis of teeth is a bad one that should be discouraged.

Biases in our Understanding of Dinosaurs

An obvious source of bias is the naming of material that is non-diagnostic, as in the case of isolated teeth. About 20% of dinosaur genera are known from essentially complete skulls and skeletons, and 57% are known from complete or partial skulls. However, hundreds of dinosaur genera and species (roughly 250 genera and nearly 500 species) are doubtful, the majority of these (61%) being based on non-diagnostic specimens (Dodson, 1990a; Dodson and Dawson, 1991). It is sobering that two-thirds of all dinosaur species described are probably not valid, and that the ratio of invalid to valid genera is nearly one to one. Probably

the nadir of taxonomic practice occurred during the
pioneering decade of the 1870's, during which 50 genera of
dinosaurs were named, only 10 of which are regarded today as
valid. The ratio of invalid to valid names then was 4 to 1,
a dubious achievement indeed. Such baggage seriously
impedes the understanding of diversity in the fossil record.

There are striking geographic biases in our current
understanding of dinosaurs. About 75% of all dinosaurs
presently known come from six countries, in descending
order: the United States, Mongolia, China, England (United
Kingdom), Canada, and Argentina (Dodson, 1990a). Precise
figures become dated quickly as discoveries continue apace
from Argentina, China and Mongolia (e.g., Bonaparte, 1991;
Perle et al., 1993). It would seem that the two countries
with the greatest potential for equalling or exceeding the
United States in dinosaur diversity are China and Argentina,
for both these countries, in contrast to Mongolia and
Canada, have continental strata that span a large part of
the Mesozoic (Weishampel, 1990). The paucity of dinosaurs
in Russia and in former republics of the Soviet Union is
striking. New finds are being made (e.g., *Udanoceratops*
Kurzanov, 1992) but large parts of the enormous landmass in
question are of Paleozoic age or are crystalline shield
areas and thus will never produce dinosaurs.

Our knowledge of dinosaurs is unevenly distributed in
time as well as in space. Stratigraphic biases are also
evident. Despite the fact that dinosaurs range from the
Carnian stage of the Late Triassic to the very end of the
Late Cretaceous, a span of 163 million years, nearly half
(46%) of all dinosaurs are of Late Cretaceous age; indeed
about 40% come from the Campanian and Maastrichtian stages
that collectively represent 11% of the recorded timespan of
the dinosaurs. Certain time intervals record very few
dinosaur taxa, notably the Early to Middle Jurassic
(Pliensbachian to Bajocian stages) and the Early Cretaceous
(Berriasian through Barremian). Because of the phylogenetic
continuity beyond these gaps, it is certain that dinosaurs
existed during these intervals even though we know very
little about them. Haubold (1990) even speculated that high
diversity communities existed during these times in
unpreserved equatorial regions. It is possible or even
probable that population bottlenecks occurred during these
times. For instance, the Cloverly Formation (Aptian-Albian,
late Early Cretaceous), and its equivalents, are widely
distributed in western United States, but do not seem to
yield a very diverse dinosaur fauna compared to that of the
earlier Morrison Formation (Russell, 1989). An attempt to
estimate dinosaur diversity must involve extrapolation
across unsampled time intervals, and assumptions must be
made about diversity during the unrecorded time.

Is it probable that dinosaur diversity increased during the Cretaceous, and peaked close to the end of that period, or is it merely a passive consequence of enhanced area of outcrop? It has been argued that outcrop area of rocks for each geological period is the best predictor for diversity during that period (Raup, 1976). If this were true, it would follow that there is no systematic increase in biotic diversity through time, although there is an increase in area of preserved sediments with increasing proximity to the Recent. A synthetic view is that the null hypothesis of no increase in diversity through the Phanerozoic can be rejected, but actual increase in diversity is lower than a simple tabulation of species number or area of outcrop might suggest (Signor, 1985). There is an increase in outcrop area of younger strata, but does the apparent increase in dinosaur diversity towards the end of the Cretaceous transcend that predicted by outcrop area? Apparent outcrop area increases during the Mesozoic from Jurassic to Triassic to Cretaceous while apparent dinosaur diversity increases in order from Triassic to Jurassic to Cretaceous. As dinosaurs existed for only two and one third periods, a much more powerful data set would be an array of outcrop area by stages, Carnian to Maastrichtian. No such compilations at this level of resolution exist. A further requirement is that terrestrial strata be segregated from marine strata. As a partial proxy, it might be argued that geological intervals of high eustatic sealevel would correspond to low areas of terrestrial outcrop, biotic bottlenecks, and reduced diversity (Horner et al., 1992). Conversely intervals of low eustatic sealevel would correspond to high areas of terrestrial outcrop and high diversity. If anything, this model is falsified by the observation that sealevel was lowest in the Triassic and highest at the end of the Cretaceous, and that apparent dinosaur diversity correlates positively with increasing sealevel (Haubold, 1990; Figure 2). Haubold argues that high sealevel also correlates with times of warm climate and poleward distribution of dinosaurs. Relation of dinosaur diversity to climate is a further complication because the Cretaceous temperature optimum occurred during the Early Cretaceous (Anderson, 1990).

Another factor that increased the diversity of dinosaurs in the Cretaceous is the breakup of Pangea, and the positioning of continents in positions that approximate their modern positions. This leads to endemicity of faunas, particularly of Asian and North American faunas (Holtz, 1993). Diversity is thus higher in the Late Cretaceous than in earlier times when more cosmopolitan faunas prevailed.

We recognize that our knowledge of dinosaur diversity is biased and provisional. Nonetheless, critical analysis of
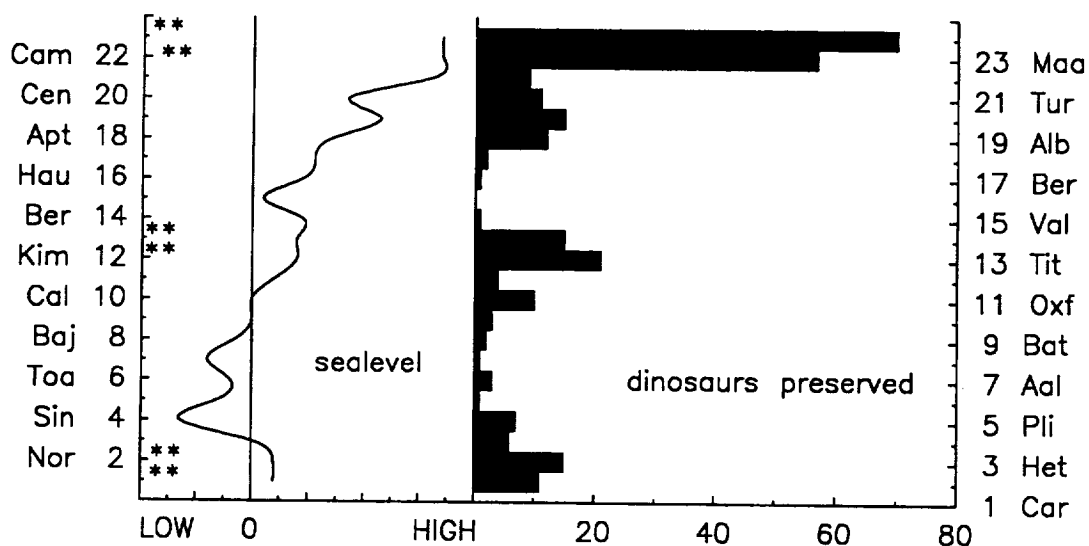
EFFECT OF RELATIVE SEALEVEL ON DINOSAUR PRESERVATION

FIGURE 2--The relationship between rising eustatic sealevel and the observed diversity of dinosaurs. The Carnian stage (1) of the Late Triassic represents the earliest stage at which dinosaurs are found, and the Maastrichtian stage (23) of the Late Cretaceous the latest stage at which dinosaurs are found.

the fossil record allows us to do several things. It is possible, making specified assumptions, to estimate the total number of dinosaurs that have ever lived. It is also possible to bring some fresh insights into the problem of dinosaur extinction.

DINOSAUR DIVERSITY

One method of estimating total dinosaur diversity requires us to know how many dinosaurs lived at one time. If that datum is known, two other data are required: the longevity of dinosaur genera, and the geometric form of the evolutionary pattern through geological time. The best known geological interval is the one most recent in geological time, the Campanian-Maastrichtian of the Late Cretaceous, from which 112 genera are recognized. Following the discussions above, this number must continue to grow as our knowledge is increased by new discoveries. Assuming this interval to be the best studied of all dinosaur-bearing strata, I would expect this number to increase to 150, and conservatively I would expect this number to be augmented by 50 further genera that will never be found due either to non-preservation or destruction by erosion. This yields a total of 200 genera of dinosaurs, or 100 per stage, that is

100 each for the Campanian and the Maastrichtian. Estimates of the longevity of dinosaur genera range from 5 million to 10.5 million years per genus, with the intermediate figure of 7.7 million years per genus held to be the most reasonable (Dodson, 1990a). The shorter figure is based on the smallest interval of geological time, and the longest estimate is based on data biased in favor of longer-ranging dinosaurs. These figures imply that the number of episodes of faunal turnover during the age of dinosaurs must range between 15 and 33, figures that seem empirically defensible. The third decision is the pattern of diversity through time. One model would be to project dinosaur diversity unchanged through time, using the latest Cretaceous as a datum. This is unrealistic. It is more realistic to tie the model to actual data, recognizing that certain intervals are relatively well sampled compared to others. The well sampled intervals include the Carnian and Norian stages of the Late Triassic through the Hettangian and Sinemurian stages of the Early Jurassic; the Kimmeridgian and Tithonian stages of the Late Jurassic; and the Campanian and Maastrichtian stages of the Late Cretaceous. A second pattern would be to assume that diversity increased monotonically as a simple cone from its lowest level in the Late Triassic to its highest level in the Late Cretaceous. A third pattern (Figure 3) is a modification of the second, but rather than assuming that diversity continued to increase after the well sampled Early Jurassic and Late Jurassic intervals, it assumes that there was an evolutionary bottleneck due to some sort of biotic stress including reduced continental landmass.

Three different longevities and three different patterns of diversity yield nine estimates that would seem to frame the possibilities for total dinosaur diversity. The estimates range from a low of 645 genera (bottleneck model, slow rate of generic turnover) to a high of 3285 genera (constant diversity, rapid generic turnover). The model of constant diversity seems completely unrealistic and so those three estimates associated with that model (1525, 2100 and 3285 genera) are eliminated. The long generic longevity also seems improbable, so those three estimates (645, 865 and 1525 genera) are also eliminated. The estimates with the greatest generality are those associated with the generic longevity of 7.7 million years or 1.1 stages per genus. The bottleneck model yields an estimate of 875 genera and the steady increase model yields an estimate of 1175 genera.

Using the assumptions stated, I estimate the total number of dinosaurs that have ever lived is probably in the range of 900 to 1200 genera. This number seems surprisingly small. If this were so, it would mean that we have now
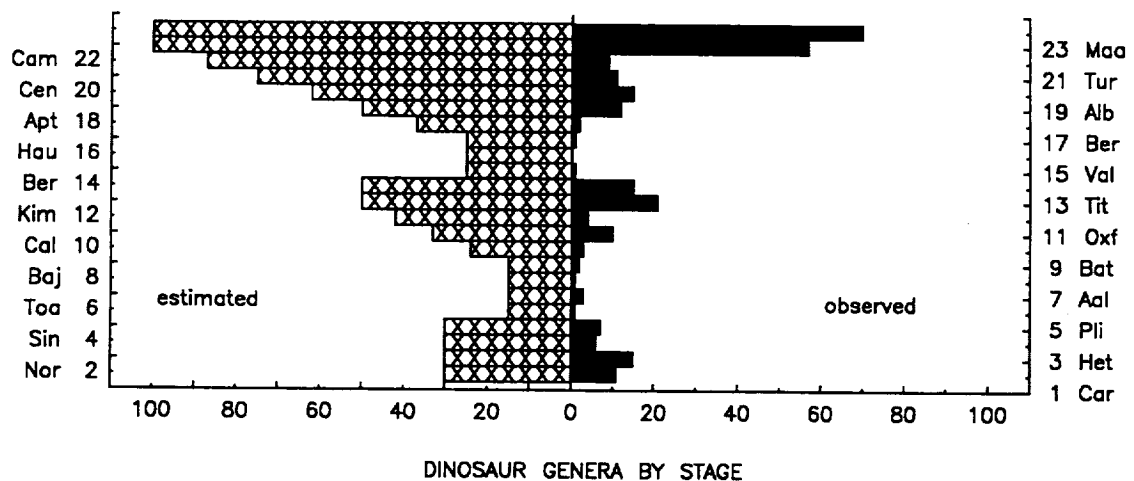
FIGURE 3--Comparison of the observed diversity of dinosaurs
(solid bars, right) through the Mesozoic with estimated
diversity with estimated diversity according to the
bottleneck model (hatched bars, left). As for Figure 2, the
oldest stage is at the bottom (1), the youngest (23) at the
top.

sampled some 25 to 33% of the fossil record of dinosaurs - a
noteworthy achievement. Signor (1985) estimated that we
have sampled about 10% of the invertebrate fossil record so
far (but 30% of the Silurian record). It is possible to
make different assumptions and achieve different estimates.
For instance, if 100 genera at any given time is too small
by a factor of two, all figures should be doubled, and the
total number would be 1800 to 2400. We would then only have
sampled 12 to 16% of the dinosaur record. There are roughly
1000 genera of mammals at present, but most mammals are
small, being rodents, insectivores, bats and others.
Ignoring these small mammals, there are 175 genera of large-
bodied mammals. It thus appears that an estimate of 100 to
200 genera of dinosaurs at any one time is reasonable.

Other assumptions can be made. It is well known that
land area is a predictor of diversity. D.A. Russell
(unpublished) has predicted dinosaur diversity on the basis
of inferred continental areas and has achieved estimates
larger than mine by a factor of three. Although the logic
behind this inference is compelling, it ascribes high
diversities to landmasses such as Antarctica where we
presently know but three taxa, all as yet unnamed. It seems
premature to attribute elevated levels of diversity to this

landmass. Another approach is that of Olshevsky (1991), who estimated that the number of dinosaur species at any one time was 6,000 and, with 33 or 34 episodes of complete faunal turnover during the Mesozoic, that a total of 200,000 species or 20,000 genera lived. The fundamental difference between Olshevsky (1991) and Dodson (1990a) is that the former believes that most dinosaurs were small. My assumption is that the dinosaurs we currently know are representative in every way of the dinosaurs we do not know. I believe that large body size (greater than 10 kg) is fundamental to dinosaur biology. There was a healthy non-dinosaurian fauna of so-called microvertebrates (less than 10 kg) throughout the Mesozoic that included mammals, lizards, amphibians and a variety of extinct types as well. Dinosaurs may have participated ontogenetically in the microvertebrate fauna, but I know of no evidence to suggest that small dinosaurs were dominant components or that the wealth of undiscovered dinosaur diversity lies there.

DINOSAUR EXTINCTION

What does our understanding of dinosaur diversity trends tell us of dinosaur extinction? Possibly nothing, although this is a pessimistic view. In a cladistic view dinosaurs have not become extinct, but rather some evolved into birds and flew away. The dinosaurs that did become extinct are a paraphyletic assemblage. (By this term a cladist designates an artificial group from which descendents have been removed, in violation of cladistic rules). The traditional concern with dinosaur extinction is thus with the paraphyletic non-avian dinosaurs. But even granted this caveat, the extinction in question is still a major one. On the one hand, the Late Cretaceous mass extinction is much broader than dinosaurs themselves, encompassing as it did vertebrates, invertebrates and plants, both in marine and terrestrial realms. On the other hand, dinosaurs have rarely figured prominently in supposedly scientific discussions of the extinction of the dinosaurs. Indeed, extraordinary claims are made under the banner of "what killed the dinosaurs?" that invoke killer asteroids or comets, without reference to dinosaurs themselves (Glen, 1990: Alvarez and Asaro, 1990; Courtillot, 1990). My purpose is not to question whether an asteroid impact occurred at the end of the Cretaceous, accounting for the famous iridium anomaly. Rather I wish to question whether the fossil record of dinosaurs supports the interpretation of sudden catastrophic disappearance or whether the fossil record is compatible with a more gradual disappearance (Archibald, 1992).

There is a large literature on both dinosaur extinction and on Late Cretaceous mass extinctions (e.g., Dodson,

1990a) that would be tedious to review. There are several reasons why the question of the cause for dinosaur extinction has not yet been laid to rest. One is that the fossil record does not directly record extinction; rather it records local events or taphonomic phenomena. Dinosaurs disappeared hundreds of times from the fossil record, but became extinct only once. Disappearance is directly observed; extinction is inferred. Another consideration is that the fossil record of dinosaurs is so poor that it is statistically almost irrelevant. A single handful of oceanic mud may contain more fossils, namely planktonic microfossils, than the entire fossil record of dinosaurs, understood to consist of articulated skeletons or partial skeletons. Thus it is natural that other organisms, especially marine invertebrates, including microfossils, figure rather more prominently in statistical analyses of extinction than do dinosaurs.

Given these considerations, what does the fossil record of dinosaurs actually show? As we saw above, dinosaurs appear to be at the peak of their diversity during the final two stages of their temporal span. There is nothing about the pattern of the fossil record that suggests that dinosaurs had reached their peak and were dwindling towards extinction. Indeed, a superficial reading of stage-level diversity data would suggest that dinosaurs were cut down unexpectedly in their prime. However, if we are investigating a claim that dinosaurs were cut down by a catastrophe of the temporal span of 10^{-2} to 10^{2} years, stage level data with a resolution of 10^{6} years are inappropriate. It is possible to some degree to resolve events within the Maastrichtian, the final stage of the Cretaceous. Maastrichtian dinosaurs are known from some 115 sites on five continents around the world age (Weishampel, 1990). Of these sites, 41 are in North America, 22 in South America, 28 in Asia (India, China and Mongolia), 23 in Europe, and 1 in Africa. However, many of these sites are of early Maastrichtian age. Only 26 sites can be documented as late Maastrichtian in age, and 20 of these are North American; 3 are from Europe and 3 from India. In the Maastrichtian as a whole, there are 73 genera of dinosaurs. In the early Maastrichtian, 61 genera are documented, but in the late Maastrichtian, only 18 genera can be recorded, and these comprise roughly 128 articulated specimens. Four genera account for 73% of all specimens. Six genera are based on more or less complete skeletal material. These are, in decreasing order of abundance: *Triceratops, Edmontosaurus, Tyrannosaurus, Thescelosaurus, Leptoceratops,* and *Ornithomimus.* Six more genera are based primarily on skulls: *Torosaurus, Stygimoloch, Ankylosaurus, Pachycephalosaurus, Nanotyrannus and Denversaurus.* All of the above dinosaurs are from western North America, in fact

primarily from Wyoming, Montana, Alberta and adjacent regions, including Saskatchewan, North and South Dakota. All of the specimens from the rest of the world are disarticulated and fragmentary. Probably the best characterized late Maastrichtian taxon from the rest of the world is *Telmatosaurus*, a hadrosaur from Romania for which 6 partial skulls are known (Weishampel et al., 1991). Also from Romania are the poorly known dwarf sauropod, *Magyarosaurus*, *Struthiosaurus*, an ankylosaur, and *Rhabdodon*, an iguanodontian. From India come *Indosaurus* and *Indosuchus*, two fragmentary theropods of uncertain family; *Lametasaurus*, an ankylosaur of uncertain family; and the enigmatic sauropod, *Titanosaurus*. From France and Spain come the sauropod *Hypselosaurus* and the iguanodontian *Rhabdodon*. Apart from *Telmatosaurus* and possibly *Rhabdodon*, no one knows what these late Maastrichtian dinosaurs looked like. Despite on-going work in France, Spain, Romania, India and China, not a single new genus of late Maastrichtian dinosaur has been described from any of these regions since 1933.

It is granted that the fossil record of late dinosaurs is very poor. Our knowledge of the last dinosaurs is incomplete and our understanding can be reversed by the discovery of a single satisfactory section that traverses the Cretaceous/Tertiary boundary anywhere in the world, including China, Argentina, or in some presently unknown terrain. The only place in the world where a reasonably healthy, moderately diverse dinosaur community can be demonstrated is in western North America, especially in the northern part of the Western Interior, centered upon Montana. Other late dinosaur faunas are fragmentary and depauperate, the European faunas representing island faunas (Weishampel, et al., 1991). In the Pyrenees region it appears that dinosaurs disappeared several hundred thousand years before the end of the Cretaceous. It is claimed that in the Hell Creek Formation of Montana, that dinosaur diversity was unreduced during the last 750,000 year interval of the Cretaceous (Sheehan et al., 1991). This claim is still a far cry from supporting a catastrophe on the time scale of 10^{-2} to 10^{2} years, but it deserves scrutiny nonetheless. The claim is made on the basis of a low resolution component of the fossil record, disarticulated teeth, cranial and postcranial skeletal bones. Such fossils are for the most part diagnostic only at the level of family, not at the level of genus or species (see above). The high resolution record of articulated skeletal material suggests that dinosaur diversity in the Hell Creek Formation was already reduced to a level of half that of the late Campanian Judith River Formation of Alberta.

It cannot be demonstrated that a single high diversity

dinosaur community existed anywhere in the world before the hypothesized terminal Cretaceous bolide impact. The Hell Creek fauna of Montana may have represented an oasis in a changing world. I do not claim to argue that a bolide impact played no role in the final extinction of dinosaurs. The impact may have been a coup de grâce. But how had dinosaurs become so vulnerable?

CONCLUSIONS

Despite the acknowledged contingent limitations of our knowledge of dinosaurs, and the fact that within 50 years we will literally know twice as much as today, there is much of which we are confident. New approaches have permitted fresh insights. Dinosaur studies during the past decade have benefitted significantly from the application of rigorous techniques of phylogenetic analysis (i.e., cladistics). The results of such studies (Weishampel, et al., 1990) are still being assimilated, and they impact on our understanding of what a dinosaur is, on their origin, the relationships of one group to another, and on whether or not they are even extinct. Another tool that has impacted on dinosaur studies is the application of statistical analyses to samples of multiple specimens. The population approach has permitted a rational basis for defining species, and also provides insights into biomechanics (Norman and Weishampel, 1985). Taphonomic studies provide critical insights into the paleoecology of dinosaurs (e.g., Rogers, 1990; Fiorillo, 1991). Studies of bone histology at last provide privileged insight into growth rates (Chinsamy, 1990, 1993).

Dinosaurs will never provide decisive data on the nature of the terminal Cretaceous extinction because they are too rare and too fragmentary to carry any decisive statistical weight. Nor are dinosaurs by their nature particularly valuable for studies of speciation. Many dinosaurs grew throughout their lives and replaced their teeth continually; they lacked small, abundant, non-replaced teeth or other decisive body parts by which mammal species can be defined. Also, Mesozoic stratigraphy rarely provides good examples of stratigraphically superimposed, fossil-bearing formations for tracing evolutionary lineages of dinosaurs. The late Campanian to late Maastrichtian formations of the Red Deer River Valley of Alberta record essentially continuous sedimentation for 11 million years, literally the best sequence in the Mesozoic. Dinosaurs are unparalleled for studies of paleobiology, broadly including functional morphology, paleophysiology and paleoecology among other disciplines. Dinosaur paleontologists typically deal with whole animals or large portions of anatomy rather than with only a few body regions. Also, because dinosaurs command the attention of artists and of the public, they present

unparalleled opportunities for science education. To
paraphrase Rogers and Hammerstein, "It's a shame for us to
worry over what they have not, we thank the Lord for all
they've got"!

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Why Dinosaurs Were Not Mammals and Vice Versa

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INTRODUCTION

Everybody knows what dinosaurs are-- or were. They were land animals which appeared first in the late Triassic, about 210 million years ago, and became extinct at the end of the Cretaceous, about 65 million years ago. They were extremely successful, being the most conspicuous and diverse terrestrial vertebrates for about 145 million years. The most impressive feature of dinosaurs is their large size, and though much is made of adult dinosaurs no bigger than a chicken, the fact remains that the smallest of these were larger than more than 70% of living mammals (Hotton, 1980).

When classified on the basis of the anatomy of their bones, as are all extinct vertebrates known only from fossils, dinosaurs turn out to be reptiles. The system works like this. Dinosaurs share the largest number of anatomical details with birds and crocodilians, so dinosaurs, birds, and crocodilians are brigaded together as Archosauria. Because archosaurs share anatomical features with a wider variety of tetrapods including lizards and turtles, all are incorporated into a more comprehensive category, Reptilia. Dinosaur thermal physiology, a favored topic of discussion, has been proposed as a basis for brigading birds and dinosaurs as a class separate from the Reptilia. This is probably not a good idea, first because dinosaur thermal physiology is secondary data, inferred from the primary data of bone anatomy. Second, thermal physiology, even if it were primary, is only one feature in opposition to the large number of documented anatomical features shared by dinosaurs, birds, and other reptiles.

Without going into detail, the ancestry of archosaurs can be traced back to animals that lived during the Early Permian, some 70 million years before dinosaurs proper made their first appearance. These animals were accompanied by early members of the synapsid lineage that ultimately gave rise to mammals, and were already anatomically very distinct from their contemporaries. Synapsids are traditionally classified as reptiles (Carroll, 1988), but should probably be raised to the level of class, coequal to and separate from the Reptilia, on the basis of their distinctive anatomy and the long history of their separateness. Stripped of jargon, this means simply that by the Early Permian, the remote ancestors of mammals and dinosaurs were already as taxonomically distinct from one another as any two groups of amniotes could be.

Attempts to restore dinosaurs on the model of living crocodilians or lizards never worked very well and were effectively abandoned about 20 years ago. It bears noting, however, that the torpid reptilian model had already taken a heavy hit more than a hundred years ago in Charles R. Knight's gorgeous restoration of two *Allosaurus*-like dinosaurs in the pose of fighting cocks. The current fashion of restoring dinosaurs after large terrestrial mammals such as elephants, rhinos, and giraffes is an improvement over the traditional reptilian model, but not by much, for dinosaurs were not mammals.

This point is established first by direct comparison of dinosaurs with living mammals, and second by tracing their respective lineages back to their beginnings. By this means we can appreciate the profound differences in their life styles and how they got that way.

For the sake of brevity we forgo a comprehensive survey of the differences between dinosaurs and mammals, to say nothing of their respective ancestors, and instead concentrate on three factors, temperature regulation, locomotion, and herbivory. Temperature regulation is included only because of its supposed bearing on locomotion. Locomotion and herbivory, on the contrary, are two features in which the contrast between dinosaurs and mammals is most striking and for which the evidence is least equivocal.

TEMPERATURE REGULATION

There is little new to be said about the supposed endothermy of dinosaurs except to suggest that it is irrelevant. Much has been made of it on the basis of the vertical posture of dinosaur limbs, and of dinosaur bone histology, but these features probably have as much to do with dinosaur size as with endothermy. To the extent that they do reflect some aspect of metabolism, they are primarily the consequence of high rates of oxidative metabolism and broad aerobic scope, of which endothermy is only a secondary manifestation. Breadth of aerobic scope is manifest in the ability to engage in prolonged high levels of activity without incurring significant oxygen debt, and in the correlated ability to repay oxygen debt quickly when it is incurred. There is little question that dinosaurs enjoyed rates of oxidative metabolism and aerobic scope greater than that of living reptiles, perhaps approaching those of birds and mammals.

Fine, but so also do flying insects such as flies, mosquitos, and dragonflies, and few are the workers who want to style as enndothermic any insects except perhaps bees (Heinrich and Esch, 1994). The secret of the ability of flies to keep beating their brains out against a window all day long, or of mosquitos to keep whining around your camp all night long, is the ability to utilize large amounts of oxygen for rapid metabolism. This ability is mediated through organelles called mitochondria, which are as densely concentrated in the flight musculature of flying

insects as in the heart muscle of birds and mammals (Gilmour, 1965). It seems that such concentration of oxygen-metabolizing units tends to elevate temperatures locally, independently of the muscle-mediated process of shivering. In a mammal of mouse size or larger, the heat so generated is conserved to produce endothermy. Incidentally, this mechanism doesn't seem to work for most birds, whose internal heat is generated primarily by the action of the muscles using the oxygen (Gordon, 1972; but for penguins see Duchamp, 1991). It is true that mammals and birds have evolved mechanisms to conserve the high body heat to which they have become adapted, but the significant point is that high body temperature is secondary to enhanced rates of oxidative metabolism.

Enhanced oxidative metabolism enables an animal to get started more quickly and to keep going longer, advantageous to prey and predator alike, but it entails the cost of greater food requirements and more continuous foraging. This is therefore not necessarily a superior mode of life, but simply a different one. The alternative, requiring far less oxygen, was probably characteristic of ancestors that lived in aquatic environments where oxygen tension is lower than on land. Living reptiles, and presumably their Early Permian ancestors, apparently never took up the habit of using more oxygen even after they had moved onto land where more oxygen was available. Such conservatism has its own advantages, not only because of its lower cost, but also because even tetrapods that breathe air as adults must spend their embryonic or fetal life at lower oxygen tension.

LOCOMOTION

Dinosaurs and mammals.-- Trackways show that in dinosaurs as in mammals the transverse distance between placement of right and left feet was very small, feet of opposite sides tracking in nearly a straight line, in contrast to the wider spread of the feet in lizards and turtles. The motion of the femur is parasagittal, largely restricted to a vertical plane parallel to and close to the midline. Anatomically this is accomplished by the articular surface of the femur at the hip being inflected, or oriented at right angles to the femoral shaft, which brings the footfall to a point directly below the hip joint.

In all dinosaurs and in very large terrestrial mammals such as elephants this condition is accompanied by vertical orientation of the femur, and is often referred to as "erect posture" (Bakker, 1971) or "vertical limb posture" (Charig, 1972). The vertical posture of the femur of elephantine mammals is apparently a graviportal, or weight-bearing specialization, for in smaller mammals the femur is carried more nearly horizontally, though it still swings through a parasagittal arc. There is no question that a vertical femur can serve a graviportal function, but in dinosaurs it is probably not a graviportal specialization as such, because it is present in all dinosaurs regardless of size.
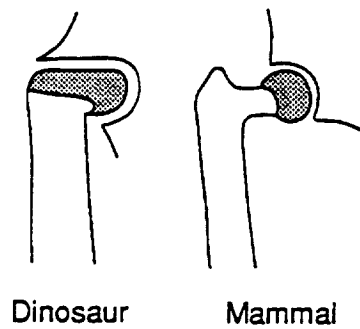
Figure 1. Femora, dinosaur and mammal. Articular end is inflected, indicating vertical posture of limb, but articulation (shaded) is cylindrical in dinosaurs and spherical (or ellipsoidal) in mammals.

Dinosaur   Mammal

This is only one of a whole suite of differences between mammals and dinosaurs in locomotor anatomy, which collectively point to profound differences in strategies of locomotion. For example, although the hip end of the femur is inflected and femoral motion accordingly parasagittal in both groups, in mammals the articular surface is spherical or ellipsoidal, whereas in dinosaurs it is cylindrical (Fig. 1). The spherical hip joint permits slight transverse displacement from the parasagittal plane, which mammals utilize for lateral adjustment of footfall while traversing rough terrain, minimizing risk of damage to the ankle joint at speed. The spherical hip joint also permits the femur to be rotated slightly about its long axis during locomotion, allowing tighter turns. Lateral adjustment of footfall and axial rotation of the femur together are fundamental to the speed and agility displayed by mammals in cursorial locomotion. In dinosaurs the cylindrical shape of the hip joint precludes all of these motions. No transverse displacement from the parasagittal plane was possible, so the only adjustment of footfall would have been fore-and-aft, in the direction of motion. The lack of transverse displacement of footfall and axial rotation of the femur would have restricted change of direction to the clumsier system of taking longer strides on one side than on the other. The net effect would be that irrespective of metabolic rates and size, dinosaurs were slower-moving and less agile than mammals. On the other hand, structure of the hip joint suggests that at constrained speeds, dinosaurs could have kept moving indefinitely. They would in fact have had to keep moving, for most dinosaurs, including the largest, were herbivores, and with their size and abundance they would have completely destroyed the flora had they been confined to a limited area.

In relative size of hind and front limbs dinosaurs are in almost diametric contrast to mammals. The hind limbs were longer than the front in nearly all dinosaurs, and trackways show that primitive forms were obligate bipedal striders-- they had no choice except to walk on their hind legs-- a pattern which persisted in all predatory forms. In ornithopods the front legs became somewhat larger, and trackways show that they walked on all fours while foraging, but moved bipedally when executing the maneuver known as getting the hell out of here. The armored stegosaurs and ankylosaurs, the horned ceratopsians, and the sauropods (Fig. 2A)
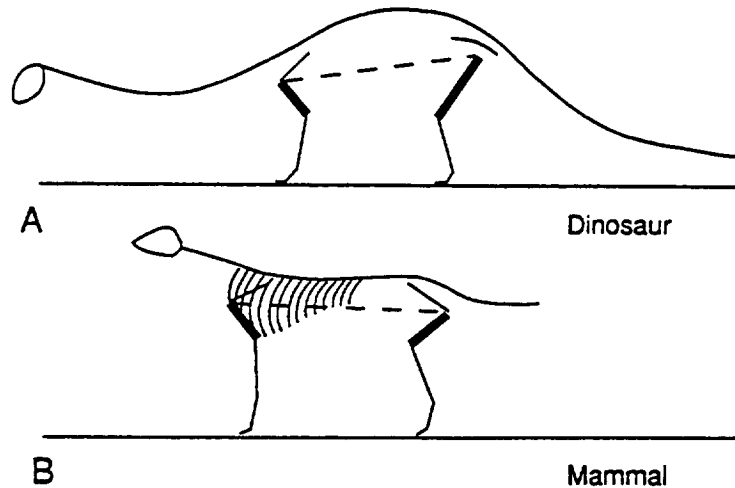
Figure 2. Limb proportions, dinosaur and mammal. A. Front limbs are shorter than hind limbs in nearly all dinosaurs, including quadrupedal forms. B. Front and hind limbs are of equal or subequal length in most quadrupedal mammals.

became obligate quadrupeds, perhaps to accomodate their great weight, but in all except the brachiosaurid sauropods the hind limbs remained longer than the front. In mammals, on the contrary, the front limbs tend to be subequal to the hind limbs in size (Fig. 2B), an inheritance from obligately quadrupedal therapsid ancestors in which locomotor emphasis was on the powerful shoulders and large front limbs. Most mammals are obligate quadrupeds, and of the few bipeds among them, all but one are jumpers or bounders-- we are the only mammalian biped that habitually strides like a bipedal dinosaur.

The contrasting anatomy of dinosaurs and mammals reflects constrasting function. In bipedal dinosaurs the hind limbs are the sole source of propulsion and the front limbs play little or no role in locomotion, whereas in quadrupedal mammals the front limbs pull the body along while the hind limbs are pushing. In quadrupedal dinosaurs the long hind limbs still seem to provide the main propulsive force, the short front limbs acting merely as idlers, to keep the animal from skidding along on its nose. Quadrupedal mammals thus appear to enjoy four-wheel drive, while quadrupedal dinosaurs are stuck with old-fashioned two-wheel drive, and rear-wheel drive at that. This difference is also manifest in the vertebral column. In dinosaurs, the short presacral column of bipedal forms plays an insignificant role in locomotion. In mammals, the proportionately elongate presacral column (Fig. 2B), by its alternate flexion and extension, shortens and lengthens the span between front and hind limbs, thereby lengthening the stride. Even when dinosaurs become quadrupedal, the presacral column remains relatively short (Fig. 2A) and rigid, as though it played little role in changing the span between front and hind limbs. These differences, in sum, emphasize the

evidence of the hip joint that life was much more leisurely and deliberate for dinosaurs than for mammals.

Antecedents.-- In functional terms, the Early Permian representatives of synapsid and reptilian lineages were not very different. Early Permian amniotes ranged from the size of living lizards to that of crocodiles, but in body form synapsids and reptiles were all much of a muchness. They were generally lizard-like, with slender bodies, long tails, and rather short but very stout limbs, front and back of equal or subequal length. The term reptile signifies "creeper", but Early Permian amniotes didn't creep, they walked; tetrapod trackways from the Late Devonian through the Permian show quadrupedal gaits, with no trace of belly-drag and only occasional traces of tail-drag.
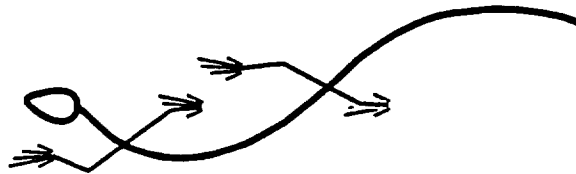
Figure 3. Gait of primitive tetrapod, "sprawled" pose. Transverse curvature of presacral column serves to increase length of stride.

In these animals the articular end of the femur is in line with the shaft; it is not inflected and the limb tended to project sideways (Fig. 3), more like the fin of a fishy ancestor than like the columnar limb of a dinosaur or mammal. Stride length was appreciably longer than would be expected from the short limbs, thanks to the presacral vertebral column, which with its massive musculature was an essential element in locomotion. With each stride the column was flexed toward the planted front foot (Fig. 3), increasing the pace length of the front feet and the span between the planted hind foot and the moving front foot of the same side.

Early Permian amniotes, e.g. the synapsid *Dimetrodon*, are usually restored with the proximal segments of the limbs directed straight out to the sides and the distal segments at right angles to the proximal, representing the so-called 'sprawled gait'. This is satisfactory as a resting pose, for these animals, like present-day lizards, probably just flopped down to rest with their limbs outstretched instead of underneath them. It does not represent limb pose during locomotion, however. If it did, the transverse distance between left and right feet would be close to the sum of the lengths of left and right femora (or humeri) plus the width of the body at the hip (or shoulder) joints. Instead, trackways show a distance between left and right feet of not more than half that. The best explanation for this

phenomenon is that as each foot was planted and the body moved forward, the trunk was rolled laterally toward the planted foot. This brought the proximal segment of the limb into a much more nearly vertical position, so that most of the animal's weight lay above the planted foot during the power stroke of the limb (Fig. 4). A similar rolling of the trunk can be observed in the characteristic
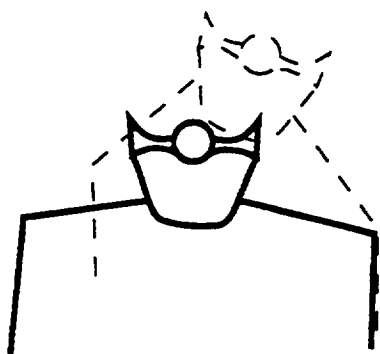
Figure 4. "Trunk-rolling" locomotor strategy of primitive tetrapods. At rest, limbs project laterally from body (solid lines), but with each stride the trunk is rolled laterally toward the planted foot (broken lines). This orients the proximal limb element more nearly vertically and brings the body weight more nearly over the propelling foot. Free limb (left side) diagrammed to indicate where foot will be planted, producing relatively narrower trackway. In reality, free limb is flung out laterally on the recovery stroke.

waddle in the quadrupedal gait of living lizards. During the forwardly directed recovery phase the limb of *Dimetrodon*, like that of lizards, moved in a transverse plane rather than a parasagittal plane. It would have looked as though it were being flung out to the side, in a sort of sidestroke, instead of being moved forward under the body. In animals with this kind of gait, Early Permian amniotes and living lizards alike, the feet are distinctively splayed, with the fifth digit shortest, the fourth longest, and digital length declining down to the short first digit.

If it exists at all, the traditional (and hypothetical) sprawled gait, with the proximal limb segment horizontal, must be restricted to some turtles, where it may be necessary to allow the shank and feet to clear the bony plastron. In any case it uses muscular effort much less effectively than the observed reptilian trick of rolling the trunk over the foot during the power stroke. In the traditional sprawled gait much effort must be expended to maintain the horizontal attitude of the proximal limb segment in order to support the body's weight, an effort which does not contribute in the least to moving the body forward. In the trunk-rolling strategy, the lateral component of motion which does not contribute directly to forward motion is minimal, and its effect is to bring the proximal segment of the limb into a nearly vertical attitude. With the proximal limb segment nearly vertical, most of the body's weight is supported passively, and most of the muscular effort can then go to moving the body forward.

The vertical limb pose of dinosaurs has been utilized as evidence of dinosaur endothermy, by analogy with the co-occurrence of vertical limb posture and endothermy in living mammals and birds (Bakker, 1971). But even in primitive ectothermic amniotes, trunk-rolling manifests near-vertical limb posture with every stride. It seems possible to extend the duration of vertical posture simply by evolving an inflected femur, without any change in aerobic scope or thermoregulation. A hypothetical ectotherm with vertical limb posture need have no trouble on account of its narrow aerobic scope, for it could stop to rest at any time by folding its legs underneath itself instead of leaving them splayed out to the sides.

Something very like this scenario seems to have taken place in the synapsids at the end of the Early Permian, when the primitive Order Pelycosauria was replaced by the advanced Order Therapsida. Pelycosaurs, as already noted by reference to *Dimetrodon*, were trunk-rollers like their contemporaries, and included the ancestors of the therapsids. In the earliest clearly characterized therapsids the limbs are distinguished from those of pelycosaurs by a femur with an inflected articular surface, and by feet in which the first digit is short but all others are subequal in length. Therapsid trackways are not especially well represented in the record, but they show that although the feet of opposite sides do not track in a nearly single line as do those of dinosaurs and mammals, they fall proportionately less than half as far apart as the feet of pelycosaurs. There is no strong consensus about the metabolic scope of therapsids, except perhaps that it was broader than that of pelycosaurs. That was not necessarily very broad, and the earliest therapsids may have been such animals as described above; no more than incipiently endothermic, they had nevertheless established locomotion with limbs in full-time vertical orientation.

The first members of the Superorder Archosauria, to which dinosaurs belong, did not appear until the Late Permian, and the first dinosaurs not until late in the Middle Triassic. The first archosaurs were lizard-like and vaguely crocodile-like animals of small to moderate size, quadrupedal and with an old-fashioned, essentially lizard-like gait. They were originally inconspicuous members of a terrestrial fauna that was dominated by therapsids, but diversified quickly. By the Early Triassic archosaurs were producing terrestrial animals as big as moderate-sized dinosaurs, including herbivores as well as predators whose jaws and teeth rivaled those of the later carnosaurian dinosaurs. Some of these animals, such as the moderate-sized *Euparkeria*, retained a primitive trunk-rolling gait, but appears to have been facultatively bipedal, like the living collared lizard of Texas. Most of the Triassic archosaurs, however, were quadrupedal, no matter whether herbivore or predator, small or large, and gaits varied all over the lot. Many had a crocodile-like gait, carrying the body high, but having an uninflected femur still utilized the trunk-rolling strategy. Others with an uninflected femur nevertheless achieved vertical limb posture by rotating the acetabulum to the bottom of the pelvis, where it faced downward. A few pre-dinosaurian archosaurs had a clearly

inflected femur with a cylindrical articular surface and enjoyed a dinosaur-like gait, albeit still quadrupedal. The first true dinosaurs were very small, bipedal, and had the same locomotor anatomy, which remained characteristic of dinosaurs until their extinction at the end of the Cretaceous.

It is a popular view that the previously dominant therapsids got their comeuppance because of competition with dinosaurs, and that a major advantage for dinosaurs in this competition was endothermy. In point of fact, however, the decline of therapsids during the Triassic coincides with the spectacular radiation of pre-dinosaurian archosaurs, and except for the survival of tiny true mammals was virtually over by the time dinosaurs came on the scene. Despite the variety of successful experiments with advanced locomotion on the part of early archosaurs, few or none of these animals are credited with endothermy. By contrast, most of the therapsids which had survived to the Middle Triassic showed numerous signs of endothermy, and the mammals to which they gave rise in the Late Triassic were probably close to full mammalian endothermy. These circumstances demonstrate two common fallacies about endothermy or broad aerobic scope: on the one hand neither is a prerequisite for the origin of advanced locomotion, and on the other neither is an advantage sine qua non for competition. Conversely, neither vertical posture of the limbs nor the success of dinosaurs after the decline of therapsids is convincing evidence of mammalian style endothermy.

HERBIVORY

Dinosaurs and mammals.-- The great majority of dinosaurs, including the sauropods and prosauropods among saurischians, and all ornithischians, are regarded as herbivorous on the basis of tooth and jaw structure, tooth wear, and body bulk. This kind of evidence is indirect but is the best we can do, for the more direct evidence provided by stomach contents and coprolites is not very useful in the study of extinct animals. The odds against finding stomach contents in place in a complete skeleton are astronomical, and coprolites composed of vegetable debris do not preserve well and are rare at all levels of the fossil record. With coprolites one has the additional problem of whodunit.

The presence of wear on the teeth indicates that the fodder was coarse, fibrous, and tough, that it was loaded with small concentrations of silica called phytoliths, or that it grew close to the ground and so was commonly covered with abrasive dust. This does not sound like a very appetizing diet, but all of the above are characteristic of living grasses, and we know how important grasses have been and still are in the success and diversity of living mammalian ungulates. An additional disadvantage of high-fiber forage like grass is that it is not very nutritious, but living mammals compensate by processing enormous amounts, which are then digested by fermentation in the capacious gut. Grasses, of course, were not on the menu of dinosaurs because they only appeared near the end of the Cretaceous

and did not become widespread until long after the dinosaurs had become extinct.

Mesozoic plants that were available for the delectation of dinosaurs were, in rough order of distance of productivity from the ground: mosses and liverworts, lycopods, ground ferns, horsetails, cycads, tree ferns, seed ferns, and conifers. The earliest angiosperms appear about the beginning of the Late Cretaceous (Doyle and Hickey, 1976), at first as low shrubby plants but producing trees before the end of the Mesozoic. The associated change in the Mesozoic flora has been implicated in dinosaur extinction, but in fact diversity of dinosaurs increased after the appearance of angiosperms and apparently remained high until the end of the Cretaceous.

A few sauropods such as *Brachiosaurus* doubtless fed at the highest levels. In that genus, unlike all other quadrupedal dinosaurs, the front limbs were longer
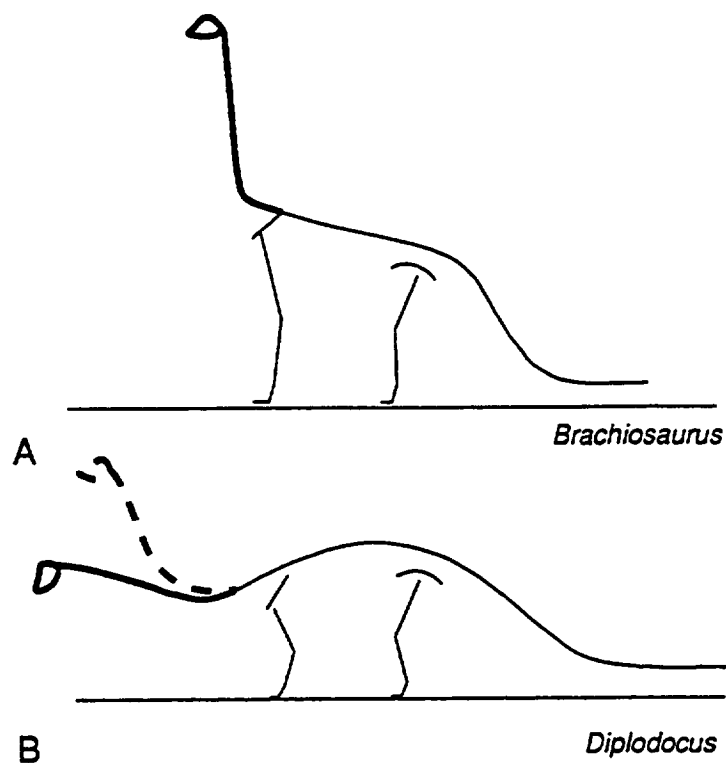
Figure 5. Contrast between *Brachiosaurus* (A), with front limbs longer than hind limbs, and more "normal" sauropod e. g. *Diplodocus* (B). Neck of *Brachiosaurus* was habitually carried vertically, atop the tall shoulder region, while that of *Diplodocus* was slung in a catenary that curved downward from the low shoulder. Maximum height to which *Diplodocus* could raise its head (B, broken line) was limited by the need to shorten the radius of the habitual curve of the neck.

than the hindlimbs, and cervical anatomy indicates that the neck rose vertically from the shoulders, as in giraffes (Fig. 5A). Restorations that show sauropods such as *Diplodocus* and *Apatosaurus* feeding in a giraffe-like manner are anatomically unsound. The shape of the neck vertebrae in these animals suggest that the neck was habitually suspended in a catenary curve. The head could be raised only by tightening the curve, and so much of the length of the neck was expended in this process that the head could be raised only a little higher than the highest point on the body, at the hips (Fig. 5B). It is likely that *Diplodocus* and *Apatosaurus* browsed most often close to the ground, and the length of the neck served to let them crop a very respectable area without moving the heavy body (Hotton, 1963; Coe et al, 1987; Dodson, 1990). Like most dinosaurs, they did their thing on the cheap. Quadrupedal trackways suggest that duckbills, iguanodonts, and camptosaurs commonly fed close to the ground, but in a bipedal stance they were tall enough to have reached the lower branches of conifers. That some of them did so on occasion is indicated by stomach contents of conifer needles in a duckbill (Krausel, 1922). Of the remaining herbivores, stegosaurs and ankylosaurs probably fed close to the ground, as indicated by their squat stance and short necks.

In most herbivorous dinosaurs the jaw joint is a simple hinge which allowed little fore-and-aft motion of the jaw. Sauropods apparently used their teeth primarily to strip foliage from trees and shrubs or from low-growing herbaceous plants, and the material was then formed into a bolus and swallowed without further processing in the mouth. The food may have been further comminuted by silicious pebbles sequestered in a muscular, gizzard-like stomach, but the evidence for such a mechanism remains equivocal. Ornithischians did more mechanical smashing-up of the food in the mouth. Such forms as stegosaurs and iguanodonts, with a single row of teeth that resemble the teeth of living herbivorous iguanid lizards, probably managed as iguanids do, chopping the fodder fairly fine before swallowing it. In advanced ceratopsians and duckbills the jaw joint allowed signifant fore-and-aft motion, and multiple closely appressed rows of teeth were functional at the same time. Athough the crowns of the teeth are worn into what looks like a grinding surface, the mechanism apparently functioned primarily in shearing (Ostrom, 1961, 1966). The greatest force on the teeth was exerted as the jaw was drawn backward during closure, forward motion being restricted to the opening of the jaw and serving primarily for recovery.

These mechanisms bore no close resemblance to the feeding mechanisms of herbivorous mammals. In mammals the jaw is capable of side-to-side as well as fore-and-aft motion, and great force can be exerted on the teeth in all directions of motion. By this means mammals can grind their food as well as shearing and chopping it, activities which collectively constitute chewing. Chewing is possible for mammals largely because of the presence of a masseter group of muscles, whose fibers run approximately at right angles to most of the remaining adductors.

Reptiles, including dinosaurs, lack an analogue of the masseter group and are incapable of chewing in this sense.

In both dinosaurs and mammals, cellulose-rich, high-fiber vegetable material is broken down in the gut by fermentation mediated by microbial endosymbionts, more effectively the more finely divided the fodder is by the time it reaches the gut. Since mammalian chewing smashes up the food more finely than dinosaur comminuting procedures, it may be assumed that mammals get more energy from a given amount of fodder than dinosaurs did. This implies that, other factors of feeding being equal, energy requirements of dinosaurs were significantly lower than those of mammals.

Antecedents.-- The following is abbreviated and paraphrased from work in progress which was initiated by J. R. Beerbower, E. C. Olson, and the author. Dinosaur faunas were heavily dominated by herbivores in a ratio of 10 or 20 to every predator, in this respect resembling present-day mammalian faunas; in Late Permian faunas dominated by therapsid synapsids a comparable ratio obtained. Before the Early Permian, however, there were no high-fiber herbivores analogous to therapsids, dinosaurs, and the later mammals. Until then most tetrapods were predators, the larger ones on other tetrapods and perhaps fish, and the smaller ones on arthropods (later on insects). By the Early Permian, a few genera recognizable as herbivores had appeared in several lineages, but collectively they were a minor part of a fauna that was still heavily dominated by predators. The Early Permian is thus a time of transition between prior tetrapod faunas that lacked herbivores and later ones that were dominated by them. Early Permian tetrapod herbivores are elements of widely divergent lineages, showing that their herbivory, like that of their successors, was of multiple independent origin.

The most generally accepted candidates for herbivory among Early Permian tetrapods are: *Diadectes* and related comparable morphotypes, *Edaphosaurus*, *Bolosaurus*, and caseid pelycosaurs. These animals qualify as herbivores from their first appearance, but a separate lineage, represented by *Captorhinus* and two allied genera have become progressively more clearly herbivorous during the Early Permian. Putative herbivores of the Early Permian represent at least 5 families in two (or three) unrelated lineages (Carroll, 1988). There is little consensus as to whether *Diadectes* is an amphibian or reptile. *Edaphosaurus* and the caseids represent respectively two families of pelycosaurian synapsids, while *Bolosaurus* represents one family of captorhinomorph reptiles and *Captorhinus* another.

The caseids, *Diadectes*, and *Edaphosaurus* are among the largest animals of their time, matching in size such contemporary top predators as *Dimetrodon*. *Edaphosaurus* (estimated maximum weight 186 kg, Romer and Price, 1940) and *Diadectes* are comparable to large alligators in size. *Captorhinus*, and *Bolosaurus* are much smaller, comparable in size to the smallest pelycosaurian predators.

Their size can be best visualized by comparison with living herbivorous iguanid lizards, *Captorhinus* with *Sauromalus* and *Bolosaurus* with *Dipsosaurus*.

All of the Early Permian putative herbivores are of sprawled 'reptilian' posture. In most the limbs are proportionately robust, as though agility and speed were not important in the gathering of food that couldn't run away. Large size would have reduced the need for agility in avoiding predation by putting adult herbivores out of reach of all but the largest predators, but it would have made little difference to the young. In the smallest Early Permian herbivore, *Bolosaurus*, the limbs were evidently longer and slimmer than those of most of its contemporaries (Watson, 1954), suggesting emphasis on speed and agility as a means of avoiding predation.

In the interest of brevity we may concentrate on the genera *Diadectes*, *Bolosaurus*, and *Edaphosaurus* (DBE), which show most clearly the differences from all contemporary predators that may be interpreted as evidence of herbivory. These differences include heavy and distinctive wear on the teeth, dental morphology, and jaw structure and motion.

Wear facets are well developed on nearly all teeth in all three genera of DBE, and absent in predators such as sphenacodonts. In putative herbivores, wear facets reflect complete removal of the enamel layer and are scoured deeply into the dentine (Figs. 6, 7). The edges of enamel surrounding the exposed dentine appear abraded, because they fair smoothly into the dentine surface (Fig. 7A) and show the same kinds of scratches or pits that are manifest on the dentine. Wear on anterior and posterior surfaces of anterior teeth is usually manifest as elongate scratches that show slight to strong preferred orientation parallel with the long axis of the tooth (Fig. 6B). Wear on the cheek teeth is dominated by elongate scratches having preferred orientation parallel with the long axis of the jaw (Fig. 7A, B).

Figure 6. *Diadectes* front tooth, wear facet. A. Back surface, upper tooth.
  B. Same, higher magnification to show scratches parallel with long axis of tooth.

Figure 7. *Diadectes* cheek tooth. A. Crown worn off; note surrounding enamel worn evenly with softer dentine. B. Same, higher magnification to show scratches parallel with long axis of jaw.

Figure 8. Sphenacodont teeth. A. Apparent wear facets on crowns. B. Posterior tooth at higher magnification; note ragged, unworn appearance of enamel layer; no scratches evident on dentine surface. C. Dentine layer at still higher magnification, still no scratches evident.

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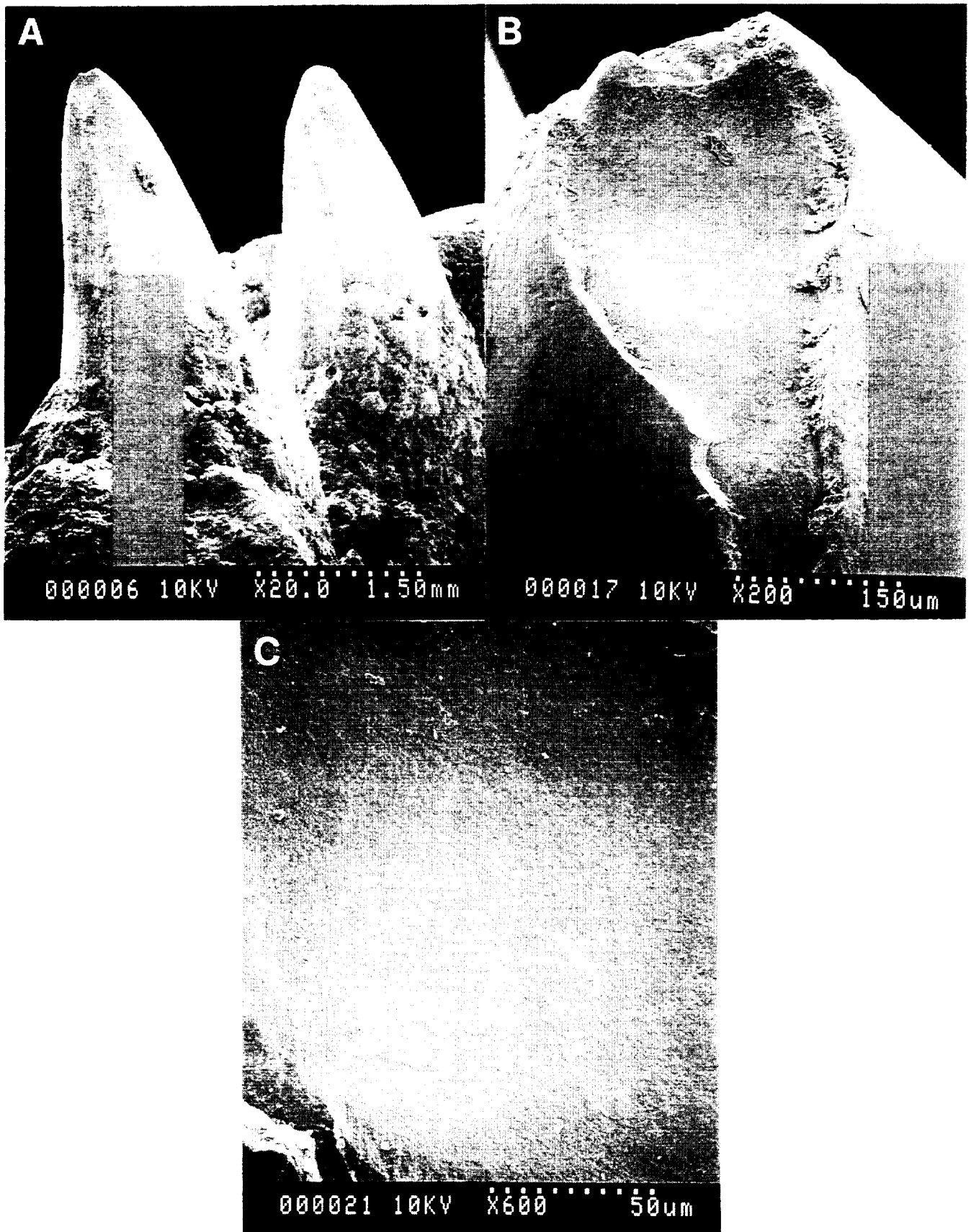
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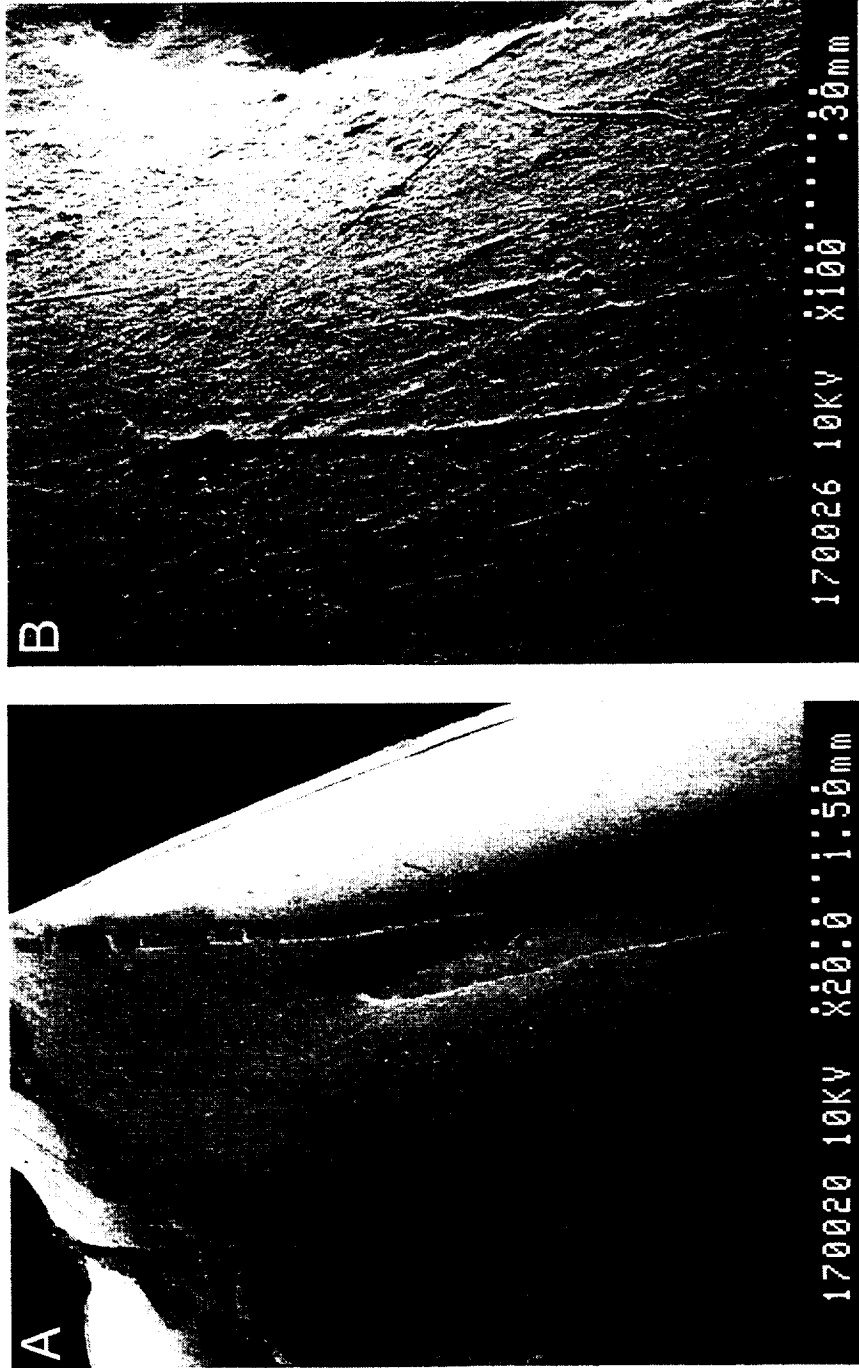
In sphenacodonts, very few teeth show exposure exposure of dentine (Fig. 8A), and in these teeth the edges of enamel surrounding the dentine are ragged (Fig. 8B), not smooth, and are not faired into the dentine. They look as though the enamel had been removed by spalling rather than wear, perhaps as a consequence of biting down on bones. Exposed dentine (Fig. 8C) seldom shows the scratches found on true wear facets.

Summarizing tooth wear, areas of exposed dentine are true wear facets in DBE and in *Captorhinus* and its allies. In all, scratches on the dentine indicate strong to moderate fore-and-aft motion of the jaw. In *Captorhinus*, a large upper front tooth consistently bears a prominent wear facet on its anterior surface, where it could not have been caused by tooth-to-tooth contact. Scratches on this facet suggest vertical motion which was probably primarily downward, actuated by neck musculature as the animal employed its anterior upper teeth in grubbing for food. In sphenacodonts, areas of exposed dentine are rare and are probably not true wear facets. Dentine surfaces appear to have been exposed by spalling rather than abrasion and are hardly scratched, and the scratches on enamel surfaces indicate primarily orthal jaw motion.

The contrast between the configuration of the jaw joint in DBE on the one hand and sphenacodonts on the other is analogous to the contrast between the joints of mammalian herbivores and carnivores. In mammalian herbivores the (squamosal) glenoid is longer than the (dentary) condyle and the joint surfaces are not closely congruent, a condition which limits gape (Hotton, 1986). In carnivores, glenoid and condyle are close to the same size and highly congruent throughout the cycle, which allows for a much wider gape. This set of relationships, together with the presence of true wear facets, suggests strongly that *Diadectes*, *Bolosaurus*, and *Edaphosaurus*, were indeed primarily herbivorous, in contrast to the predatory nature of sphenacodonts.

Since *Diadectes*, *Bolosaurus*, and *Edaphosaurus*, like all Early Permian tetrapods, were confined to a sprawled limb pose, whatever they fed on could not have grown more than a few tens of centimeters above the surface. In their proportions, notably their short, blunt faces, these animals are reminiscent of herbivorous iguanids such as *Iguana* or *Sauromalus*, and they are easily visualized as sprawled in the Permian sunshine, turning their heads this way and that as they browsed away on low-growing vegetation. Such vegetation of itself may not have been especially tough or abrasive, but growing so close to the ground it would have been covered, at least part of the time, with a great deal of abrasive silica.

What provided fodder for Early Permian herbivores is at this point anybody's guess. The best candidates are herbaceous ferns, lycopods, equisetalians, conifer seedlings, and mosses, none of which are especially nutritious and none of which are known for their productivity, at least in their current incarnation. Neither of these shortcomings, however, would have posed much of a problem in the Early

Permian, for herbivorous tetrapods, being ectotherms, would have had to process far less food than mammals do. They would have required less time to gather sufficient quantities of low-quality browse, and that interval during which they were most vulnerable to predators would be correspondingly short.

In many other tetrapods, dentitions suggest diets of animal tissue but more direct evidence indicates consumption of significant amounts of low-fiber plant material. These animals are impossible to diagnose as herbivores (or omnivores) on grounds comparable to those used to diagnose DBE and their contemporaries. *Protorosaurus*, for example, is a primitive Late Triassic archosaur with slender, recurved marginal teeth, which led Haubold and Schaumberg (1985) to diagnose it as piscivorous. Gut contents, however, are carbonaceous and include ovules of a contemporary conifer (Munk and Sues, 1993; Wiegelt, 1926), as do coprolites (Schwietzer, 1962, 1968). Thus direct evidence suggests that *Protorosaurus* was herbivorous, specializing in low-fiber plant material, though Munk and Sues (1993) conclude, conservatively, only that it was omnivorous. Similarly, many small living lizards, in which generalized dentitions suggest insectivory, are known to subsist exclusively on vegetable material for protracted periods (Greene, 1982). Such animals either do not require specialized dentitions for mechanical processing of low-fiber food, or have become herbivorous too recently to have evolved morphological features that reflect the habit. Neither do they manifest enlargement and other specializations of the gut to accomodate protracted fermentation, which perhaps is not necessary for the utilization of foodstuffs low in cellulose.

Carboniferous counterparts of these animals are usually labeled as insectivorous because of their generalized dentitions, small size, and lizard-like habitus. Many such Carboniferous 'insectivores', however, may have been omnivorous on the model of living lizards described by Greene (1982), and some may have been obligate herbivores, albeit on low-fiber plants. Pre-Permian tetrapods of lizard-like habitus are therefore the animals with greatest potential as antecedents of the herbivory that is first manifest in *Diadectes* and *Edaphosaurus*. Fossils of these animals provide no means for distinguishing dietary preferences among them, but their position in the record at least establishes constraints on the circumstances in which tetrapod herbivory first arose.

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The Place of Dinosaurs in the History of Life

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INTRODUCTION

If one were to ask a group of paleontologists "How do dinosaurs fit into the history of life on Earth?" the answers would all be different. The question is so big that it surpasses the vision of a single person, and the answers would be as diverse as those of the blind men describing an elephant from its parts. The answer which follows is also from someone who cannot see the whole "elephant." It is so simple that it is surely grossly inadequate, like lamely describing the hypnotically beautiful appearance of the Earth from space as spherical.

The position of dinosaurs in the history of life is here assessed using the exponential curve as a measuring stick. The rate of bending of such a curve is proportional to the elevation of the curve. Many biological responses, like unrestrained population growth or decline, are self-driven (accelerating or decelerating) functions of time. Natural selection is a biologic response to interactions (competition) between organisms, and it is common knowledge that evolutionary events became more frequent ("accelerated") with the passage of geologic time (Figure 1), reflecting a pattern of change similar to that of population growth. The change in biodiversity through geologic time can also (imprecisely, see below) be described by an exponential curve (Figure 2, see also Equation 1, below). This curve implies that the age of dinosaurs occurred during a midpoint in the history of biodiversity.

It is easy to understand how the physical environment affects life. Our gardens die when they dry up, or freeze. For this reason the interactions between life (including dinosaurs) and the physical environment will be described first. Then long-term changes resulting from interactions between organisms (including dinosaurs) will be described. These changes resemble those which take place when athletes run faster and faster as they compete with each other in a relay. Finally, the course of evolution will be seen as a
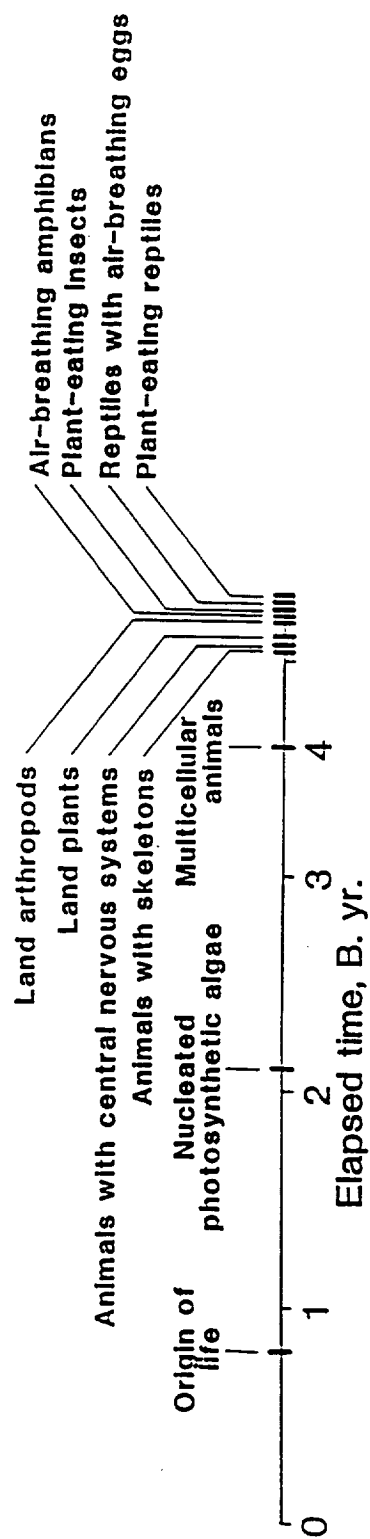
Figure 1: Distribution of significant evolutionary events through time.

compromise between exponentiating living things (including dinosaurs) and quasi-linear changes in the physical properties of the planetary surface.

THE PHYSICAL ENVIRONMENT

In an actual plot of marine diversity, the age of dinosaurs does seem largely to have coincided with a midpoint in diversity (Figure 3). However, this curve is quite irregular, and at times broadly departs from exponentiality. Thus, if the process of the diversification of life is fundamentally exponential, it has nevertheless been strongly affected by other factors.

Short-term declines in diversity were produced by mass extinctions, which are thought by people like myself to be the result of sudden physical stresses from the extraterrestrial environment, such as the impacts of comets. However, after a few million years, in each case diversity returned to former levels (Sepkoski, 1992; Figure 4A), suggesting a return to equilibrium conditions. Equilibrium conditions today are set by physical factors, and the great departure from exponentiality between 500 and 250 million years ago suggests that the gross physical environment of the planet profoundly changed during this time. Circumstantial evidence (Figure 4B-C) suggests that these changes may include a reduction in the area of shallow seas, in global temperatures, and in nutrients essential to plant growth (atmospheric carbon dioxide).

Area, temperature and nutrient availability affect diversity in land organisms today. For example, the relationship between the logarithm of land area and the logarithm of diversity is known to approximate a straight line (Figure 5). The rate of evapotranspiration in trees (Figure 6) is highly correlated with plant growth, which is in turn related to temperature, water availability and solar energy. It is also approximately linearly related to the diversity of plant species, which is in turn correlated with the diversity of animal species. The same physical factors probably affected dinosaur faunas. Note the diminishing size of dinosaurs which, approximately 110 million years ago (during middle Cretaceous time), respectively inhabited well-watered lowlands on the southern supercontinent of Gondwana, semi-arid plains within North America, and the arid interior of central Asia (Figure 7A-C).

During the earlier part of the dinosaurian era, between 250 and 100 million years ago while the diversification of
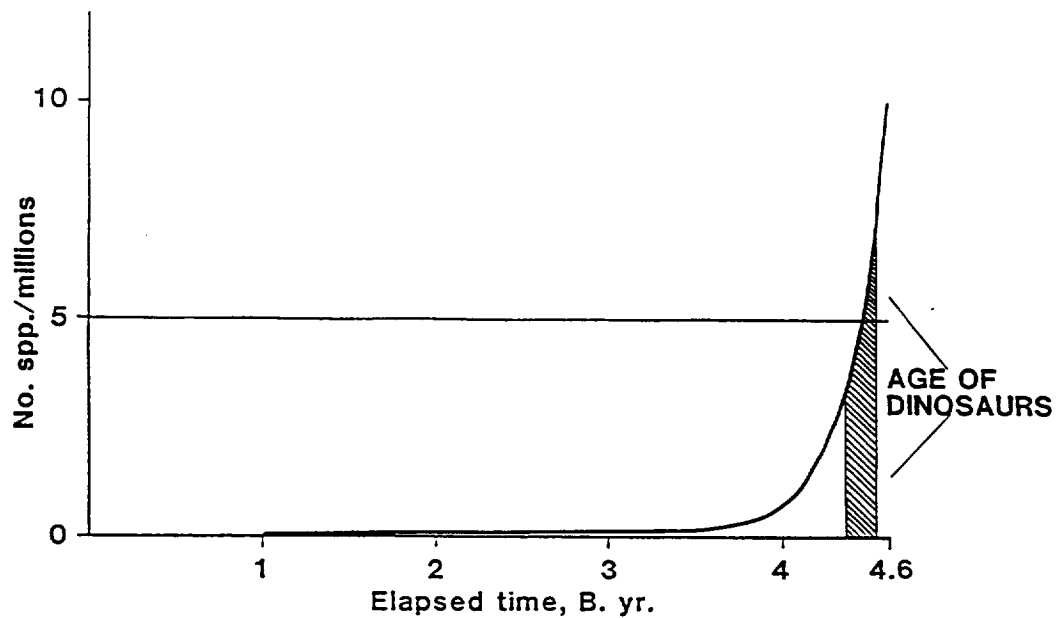
Figure 2: An exponential curve fitted to endpoints of 1 species and 10 million species (cf. May, 1992) on a geological time scale. The age of dinosaurs brackets the midpoint on the biodiversity curve.
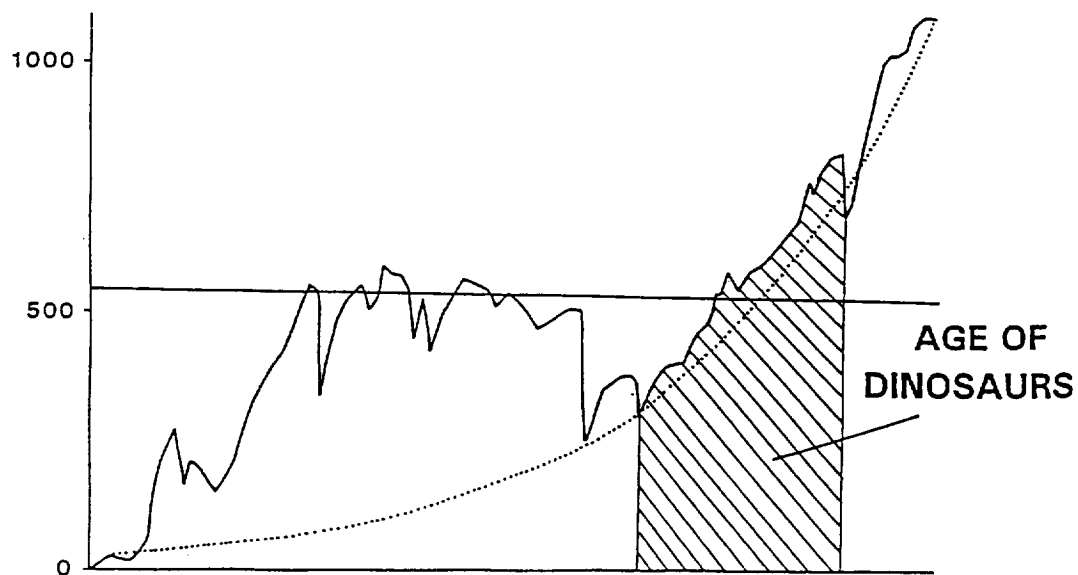
Figure 3: The age of dinosaurs indicated on a plot of the diversity of families of marine animals over the last 600 million years (modified after Sepkoski, 1993). The dotted line indicates an exponential trend in diversity.
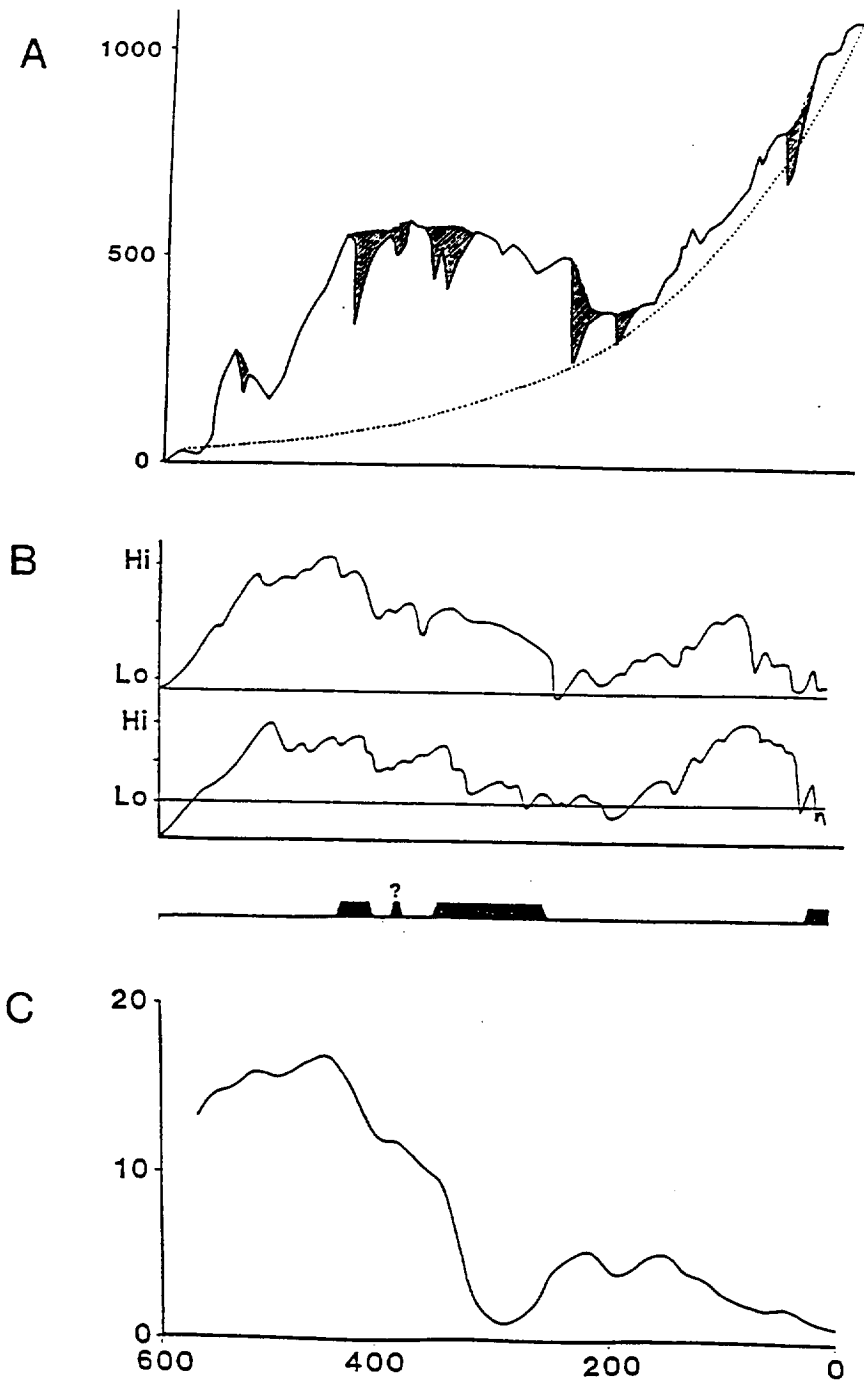
Figure 4: A - As in Figure 3, but with recovery times after mass extinctions cross-hatched; B - sea level curves and black bar representing glacial intervals (after Crowley and North, 1991); C - atmospheric carbon dioxide levels, in multiples of present atmospheric level (after Berner, 1993). The horizontal axis represents time in millions of years before the present.
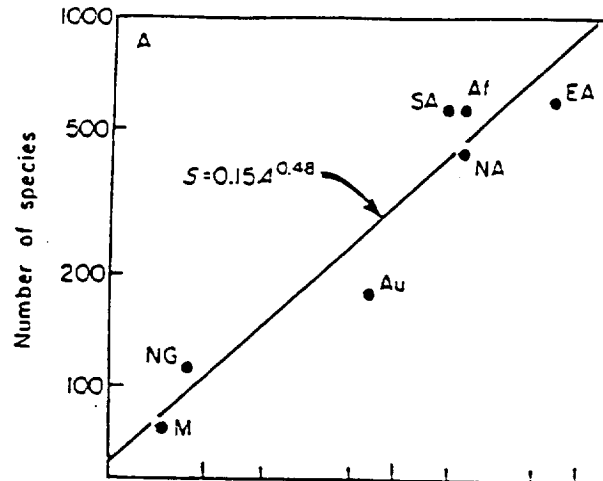
Figure 5: Area versus species diversity; Af - Africa, Au - Australia, EA - Eurasia, M - Madagascar, NA - North America, NG - New Guinea, SA - South America (after Brown, 1986).
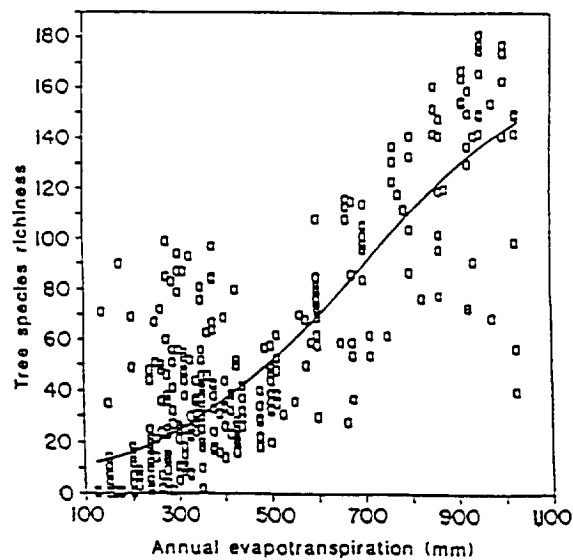
Figure 6: Number of tree species versus evapotranspiration. For further explanation see text (after Currie and Paquin, 1987).
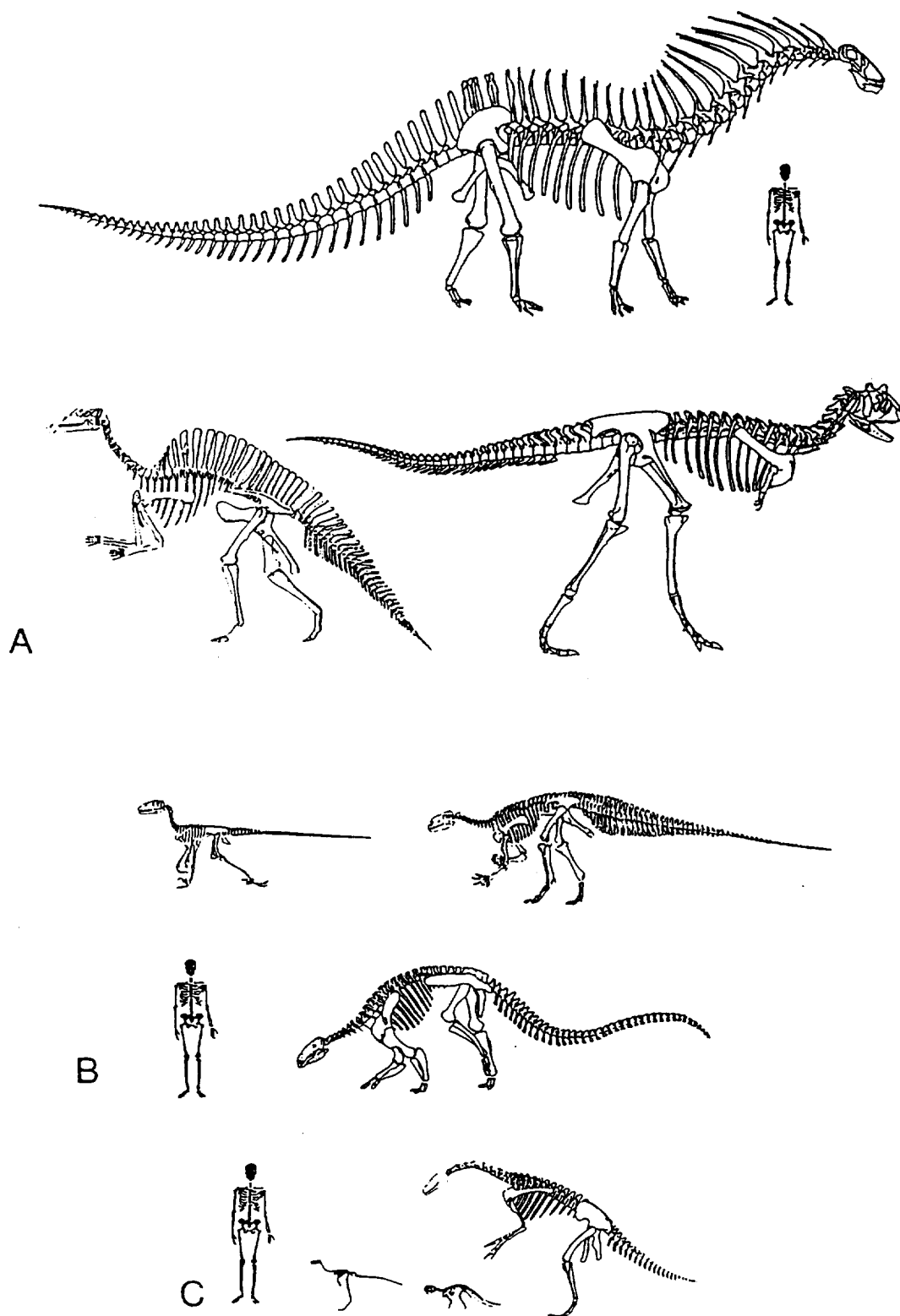
Figure 7: Skeletal reconstructions of mid-Cretaceous dinosaurs, with human skeleton for scale: A - Gondwana dinosaurs; B - North American dinosaurs; C - central Asian dinosaurs.

marine organisms was steeply increasing, the diversity of terrestrial vertebrates stagnated (Figure 8A-B). Then, during the last few tens of millions of years of the dinosaurian era, terrestrial vertebrate diversification began to increase steeply as well, parallelling a radiation of vascular plants (Knoll and Niklas, 1987). The diversification of dinosaurs appears to have followed this pattern; stagnation followed by rapid increase toward the end of the dinosaurian era (Figure 9). It is well appreciated that living tropical rain forest ecosystems represent an extreme of biodiversity. These forests occupy unusually benign environments, where temperature and rainfall are nearly optimal for life. During much of the dinosaurian era, tropical lands were reduced in area, and deserts were more widespread than at present (Zeigler et al., 1987). The equatorial regions may have been too small and too hot to sustain diverse ecosystems, and the continents as a whole may have provided a less benign home for life, resulting in a stagnation in diversification.

During the time of their greatest diversity, spanning the last 15 million years of the dinosaurian era, area-diversity relationships suggest that more than 400 basic varieties (genera) of dinosaurs should have been present on Earth (Russell, in press A). Only 111 have so far been described, and only 28 are known from relatively complete skeletal material (all of which are from either North America or Asia; Weishampel et al., 1990). Thus, reasonably complete information on the general form of but 7% of the basic varieties of dinosaurs is available for the richest portion of their record. It should be apparent that the record is too incomplete to identify unambiguously the cause of their extinction as a cometary impact. That a cometary impact was the cause is abundantly implied by trace element, isotopic, mineralogic and microfossil evidence (Hildebrand, 1993; Nichols et al., 1992; Olsson and Liu, 1993). The terrestrial record does suggest that the stresses driving dinosaurs to an abrupt planet-wide extinction were not freezing temperatures, but starvation through a collapse in the growth of green plants. This collapse may have been caused by acid rain, derived from sulpher-rich target rock and scorched nitrogen injected into the atmosphere in the impact.

THE BIOLOGICAL ENVIRONMENT

Marine and terrestrial fossils may be grouped into statistically discrete assemblages ("evolutionary faunas") which remained coherent through long intervals of geological

time. The old marine "Cambrian fauna" has essentially vanished (Sepkoski, 1992; Figure 8A). However, members of the marine "Paleozoic fauna" still persist in a world dominated by the marine "Modern fauna." Members of the "Paleozoic fauna" typically have lower metabolic rates, are less active, and can survive in leaner, less productive environments than can members of the "Modern fauna." They could also prosper in more productive environments, but are usually excluded from them by active predators (e.g. bony fishes) belonging to the "Modern fauna." Through geologic time the older of three "faunas" have successively been displaced from the more productive nearshore waters into less productive environments located at greater depths offshore (Aronson, 1990; Bambach, 1993; Jablonski and Bottjer, 1991; Sepkoski, 1992, Tunnicliffe, 1992). Reptiles (placodonts, ichthyosaurs, plesiosaurs, chelonians, mosasaurs), and later mammals (cetaceans, sirenians, carnivorans) have successfully re-invaded nearshore marine environments, although marine vertebrates have not re-invaded the land. The ranking of areas, in diversity as well as sources of emigrant organisms, is thus from land to pelagic-onshore to offshore to abyssal. In recent times, emigrant organisms are derived from diverse and productive ecosystems, are characterized by relatively higher metabolic rates and enlarged central nervous systems, and often carry relatively virulent pathogens (Vermeij, 1987, 1991; Lodge, 1993).

Three distinct assemblages of terrestrial vertebrates have also been delineated (Benton, 1989, Figure 8B): a late Paleozoic-Triassic "labyrinthodont amphibian, 'anapsid,' mammal-like reptile fauna," a Jurassic-Cretaceous "early diapsid, dinosaur, pterosaur fauna" and a Late Cretaceous-Cenozoic "frog, salamander, lizard, snake, turtle, crocodile, bird, mammal fauna". These "faunas" did not persist as long as did the marine "faunas," and tend to be bounded by mass extinctions. As noted above, the diversity of terrestrial vertebrates increased most rapidly during the Late Cretaceous-Cenozoic interval.

Dinosaurs became larger during early Jurassic time (between 210 and 175 million years ago), as atmospheric levels of carbon dioxide increased and plant fodder may have become more abundant (Berner, 1993; J. O. Farlow, personal communication 1993) Truly giant dinosaurs inhabited lowland environments by Late Jurassic time (150 million years ago). Yet by Late Cretaceous time (75 million years ago) dinosaurs inhabiting lowland environments were clearly smaller (Figure 10), although these environments in all probability supported equally or more luxuriant vegetation. Many Late
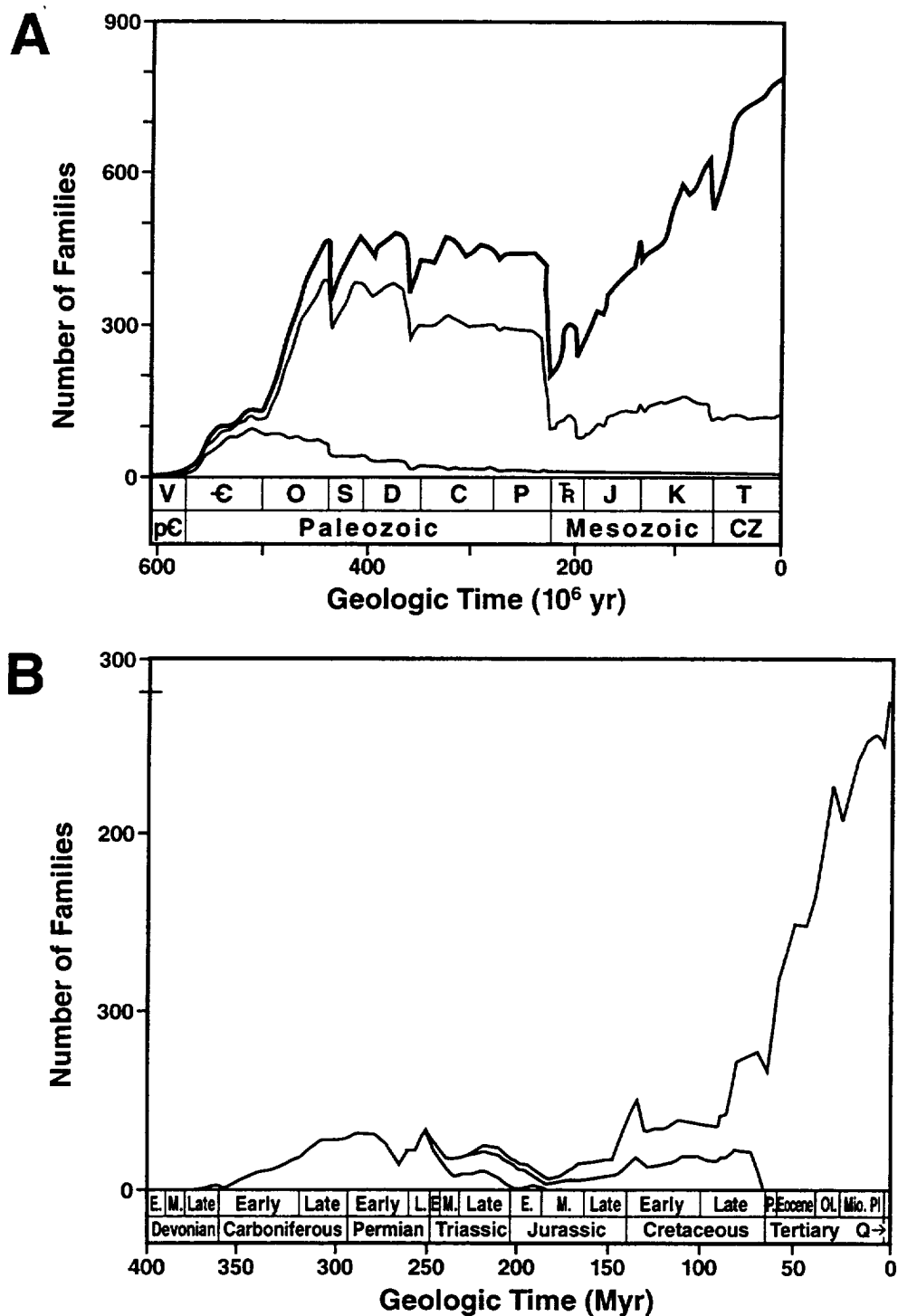
Figure 8: A - diversity of marine families through the last
600 million years, showing Cambrian (lower left curve),
Paleozoic (central curve) and Modern "evolutionary faunas"
(upper right curve, after Sepkoski, 1992); B - diversity of
families of terrestrial backboned animals, showing three
"evolutionary faunas" (after Benton, 1989).
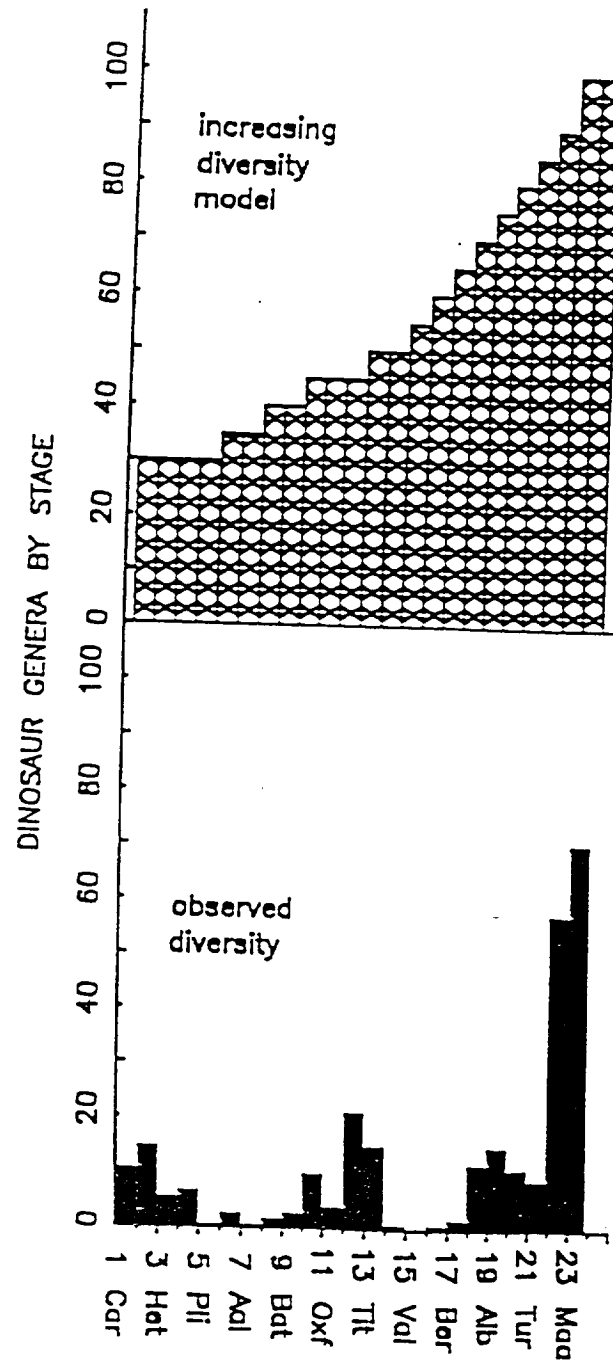
Figure 9: Diversity of dinosaurs through Late Triassic - Late Cretaceous time (modified from Dodson, 1990).
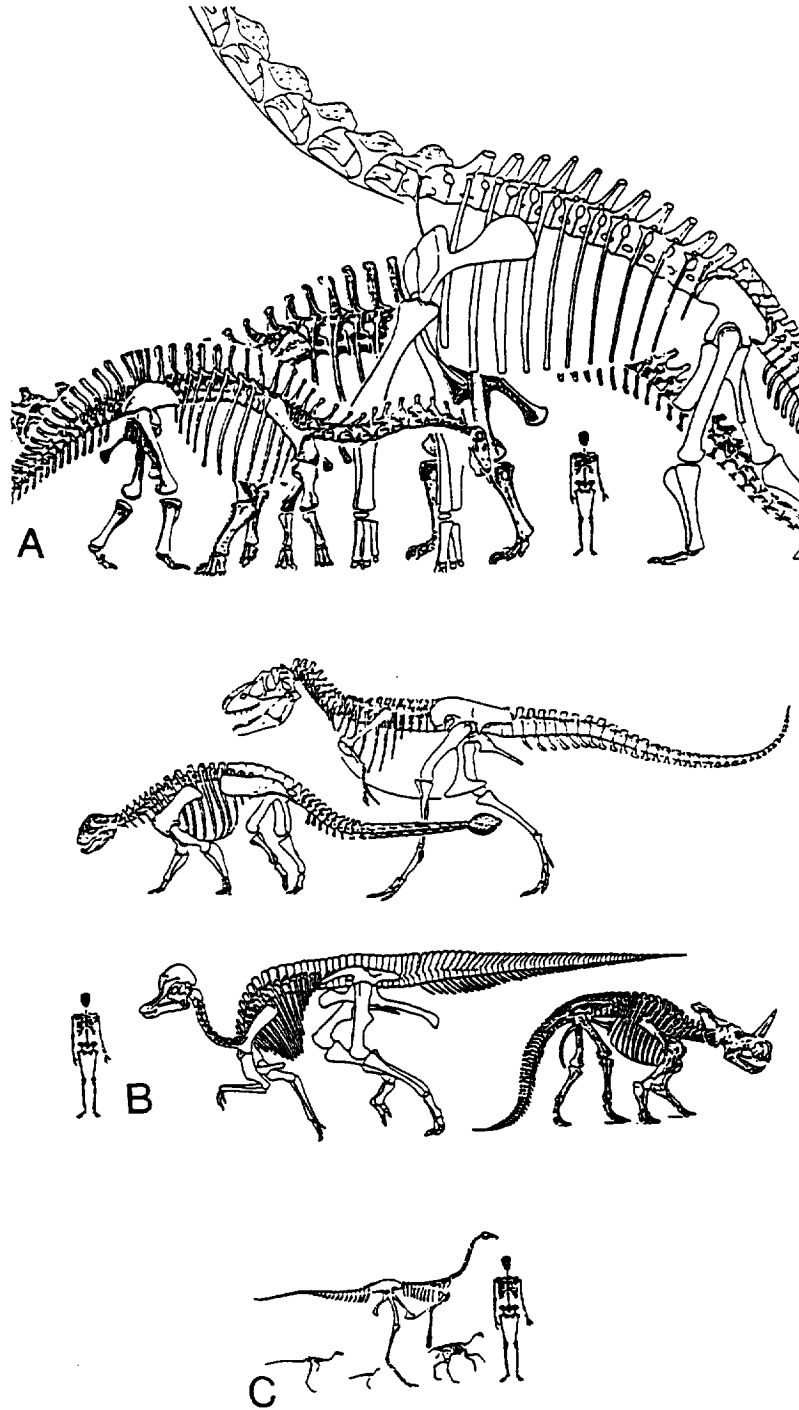
Figure 10: A - skeletal reconstructions of Late Jurassic dinosaurs, with human skeleton for scale; B - skeletal reconstructions of Late Cretaceous dinosaurs; C - skeletal reconstructions of Late Cretaceous bird-like dinosaurs.

Cretaceous dinosaurs were relatively small and rather bird-like, with long, graceful limbs suggestive of high activity levels. Indeed, other small dinosaurs had previously given rise to birds, which were able to survive the extinctions which brought the dinosaurian era to a close. It is reasonable to suspect that dinosaurs were gradually becoming smaller through geologic time.

Larger animals require less food per unit body weight to sustain themselves. It is because of this (and other) efficiencies that animals tend to become as large as their food supply permits. A "cold-blooded" brontosaur probably spent most of its time eating, just as a "warm-blooded" elephant does. However, the brontosaur was larger probably because a comparable amount of food could nourish the smaller per unit weight requirements of a body several times heavier than that of an elephant. If dinosaurs were so big because they were "cold-blooded," then if they became smaller through geologic time, it was perhaps because they were also becoming more "warm-blooded" (Russell, in press B).

One hundred and fifty million years ago, a typical (average) foliage-eating brontosaur weighed about 7,000 kilograms (Coe et al., 1985). An animal this large is almost required to be "cold-blooded" in order to avoid metabolic heat prostration. Per-kilogram food requirements, extrapolated from the trend in living reptiles (Farlow, 1976) is indicated by the lower left black dot in Figure 11. This dot is connected by a dashed line to another black dot on the upper right, which represents the per-kilogram food requirements of a typical (average) modern foliage-eating mammal weighing 200 kilograms (such as a zebra). The vertical line near the centre of the graph represents a typical (average) foliage-eating dinosaur from 75 million years ago, weighing about 2,700 kilograms. The black dots on the vertical line represent, in ascending order, the food requirements of such a dinosaur if it had the metabolic rate of a reptile ("cold-blooded"), of an Australian pouched mammal (marsupial, Hinds and McMillan, 1984), or of typical modern mammal ("warm blooded"). The open dot represents the food requirements predicted by an exponential curve (not shown) drawn through the end points, and the heavy line an exponential curve (Equation 2) calculated from the "marsupial" dot and the two end dots. The open dot and heavy line suggest that:

a) Late Cretaceous foliage-eaters (dinosaurs) were "lukewarm blooded," and
b) the food requirements of foliage-eaters increased exponentially through the last 150 million years.
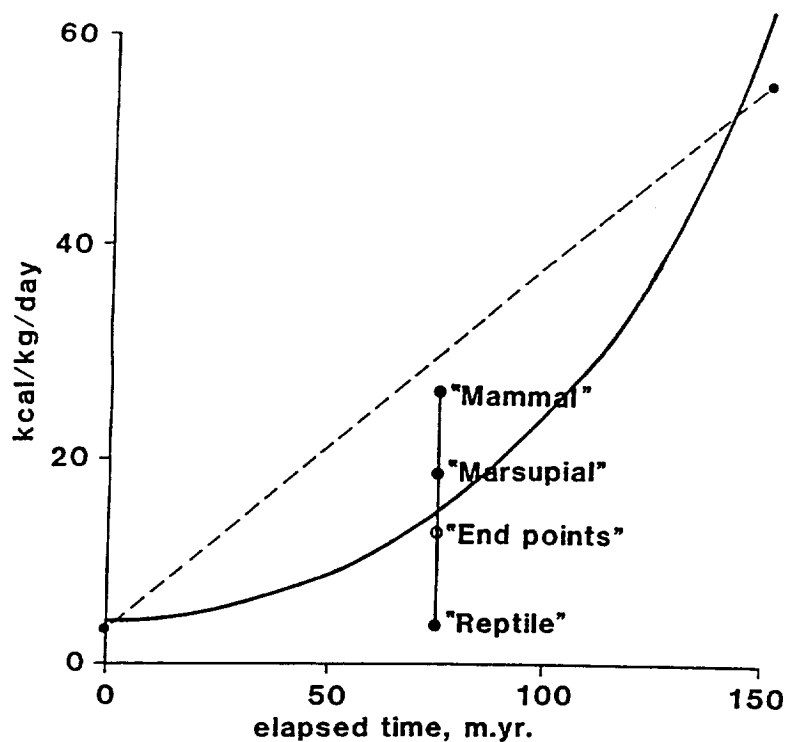
Figure 11: Food requirements of foliage-eating dinosaurs, plotted against elapsing geologic time. For further explanation see text.
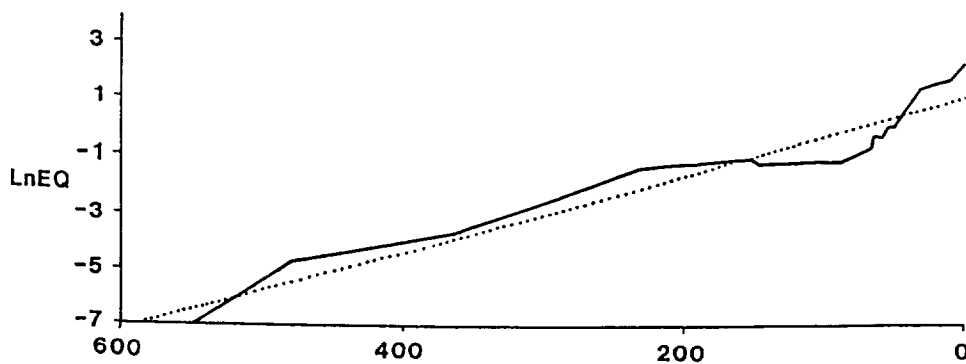
Figure 12: Maximum brain weight corrected for body weight effects ("encephalization") plotted against geologic time.
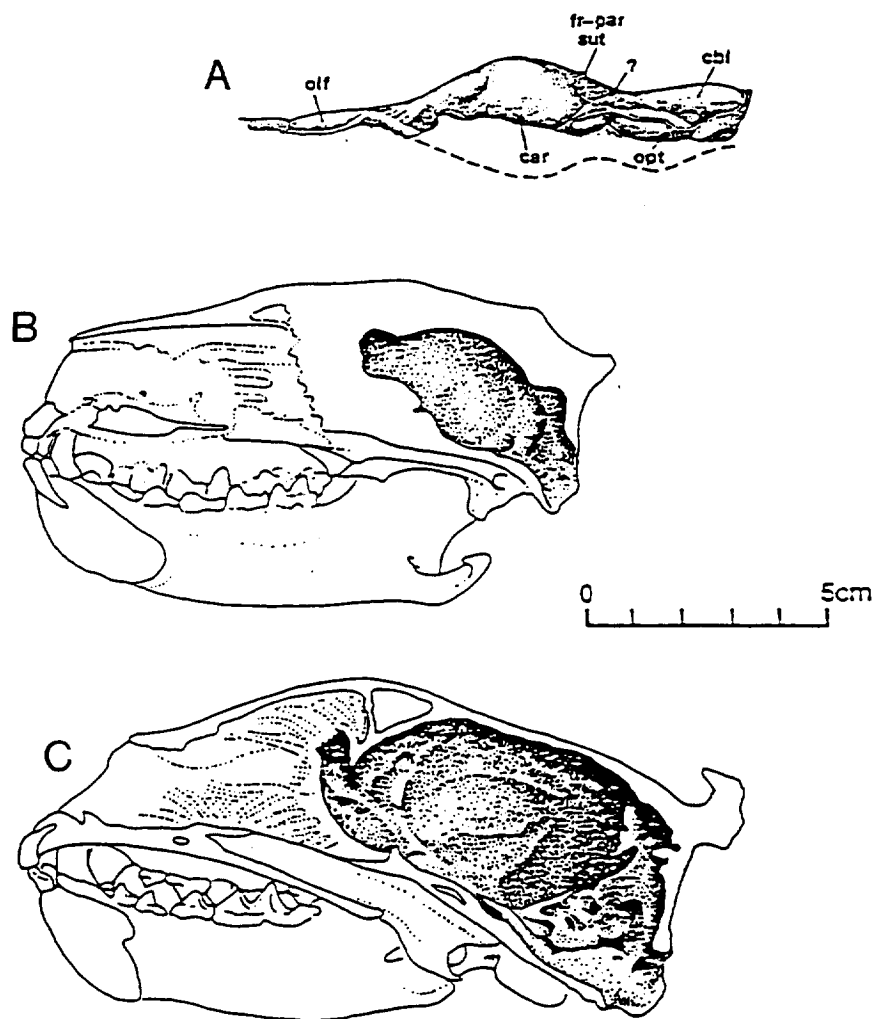
Figure 13: A - endocranial cast of <u>Troodon</u> (after Hopson, 1979); B -endocranial cavity of a Tasmanian devil; C - endocranial cavity of a wolverine (B and C after Murray, 1991).
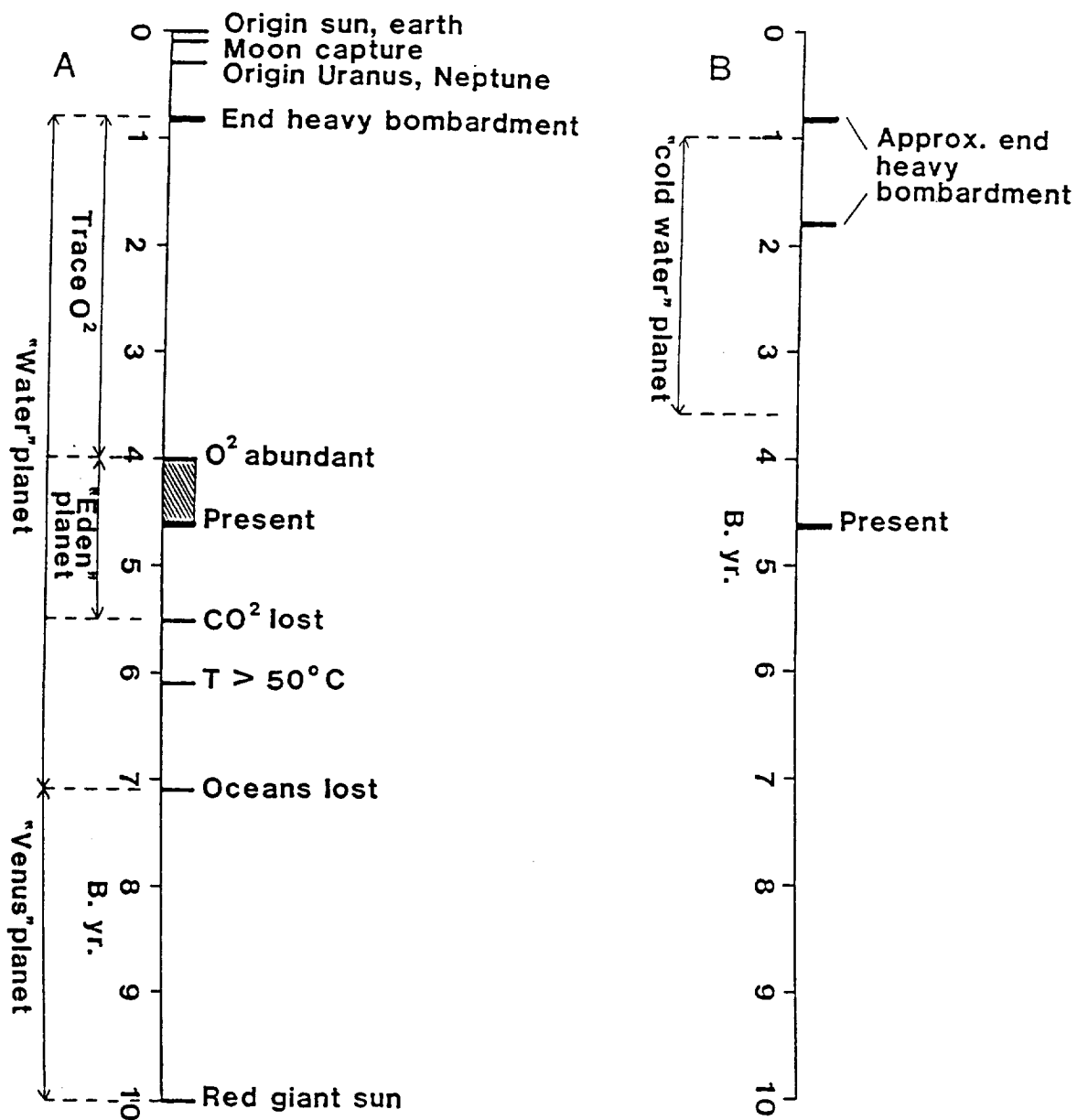
Figure 14: A - Significant physical environmental changes during the history of Earth plotted against elapsing geologic time measured in billions of years (for data see Caldeira and Kasting, 1992, and references cited therein); B - Significant physical environmental changes in the history of Mars (for data see Baker et al., 1991, and references cited therin). Note that the cold oceans of Mars probably never provided a hospitable environment for the rapid evolution of multicellular organisms.

The maximum weight of the central nervous system in backboned animals (corrected for body size effects) has increased through geologic time (Russell, 1983; Wyles et al., 1983), and the trend closely resembles an exponential curve (Figure 12; the curve described by Equation 3 for the average weight of the central nervous systems in backboned animals is similar but slightly flatter). Interestingly, the flattest part of the curve corresponds to the earlier part of the dinosaurian era, when the equatorial regions of the Earth were arid and the diversification of life on land had stagnated. However, dinosaurs participated in the more general trend. A brain cast of an exceptionally large brained small Late Cretaceous dinosaur (*Troodon*, Figure 13A) is about as large as the brain cavity in a typical Australian marsupial (Tasmanian devil, Fig 13B), but both are smaller than the brain cavity of a typical modern mammal (wolverine, Figure 13C). All three animals weighed about 30 kilograms.

On the average, Australian pouched mammals have lower metabolic rates and smaller brains than do the more typical mammals from the northern continents (Hinds and McMillan, 1984; Murray, 1991). Late Cretaceous dinosaurs probably did not surpass Australian pouched mammals in either of these attributes, and may even have possessed them to a slightly lesser degree. The Australian faunas sustained heavier extinctions after the ice age than did those of the northern continents, and remain threatened today by northern invaders. It might be predicted that Cretaceous dinosaurs, too, would have suffered in competition with modern terrestrial backboned animals, and that, by analogy, Jurassic dinosaurs would have suffered in competition with Cretaceous dinosaurs. The notion that dinosaurs were slower and more stupid than depicted in recent "hot-blooded" restorations may offend some tastes. However, it does not seem likely that the denizens of the fabled Isla Nebular in Michael Crichton's "Jurassic Park" would have posed a serious threat to ecosystems on the Central American mainland, much less to human civilization.

CONCLUSIONS

Fitness appears to be correlated with biodiversity, activity levels (metabolic rate) and behavioural flexibility (relative size of the central nervous system). Measures of these three variables are apparently accelerating functions of time. Fitting an exponential curve to the appearance of a single species of multicellular organism ("Metazoan") 700 million years ago and 10 million species of multicellular

organisms assumed now to be present on Earth (May, 1992) yields (T, elapsed time in millions of years):

Equation 1:
$$\text{Metazoan diversity (species)} = e^{0.023T}$$

As discussed above, curves describing the food requirements of foliage-eating backboned animals ("Tetrapod metabolism," Equation 2) and the average weight of the central nervous system in backboned animals, corrected for body size effects ("Encephalization," Equation 3) may be similarly approximated:

Equation 2:
$$\text{Tetrapod metabolism (kcal/kg/day)} = 3.7e^{0.019T}$$
Equation 3:
$$\text{Encephalization (average)} = 0.001e^{0.013T}$$

Intuitively, it would seem that the concept of "fitness" is of more fundamental importance in inter-organismal competition and natural selection than is the concept of "complexity" (cf. Ruse, 1993). Organismal "complexity" is difficult to measure. However, the foregoing correlates of "fitness" reveal how it changes with respect to time. Accordingly, "Fitness" is here postulated to be an autocatalytic process approximated (averaging the constants in Equations 1-3) by:

Equation 4: $$\text{FITNESS} \approx 1.2e^{0.018T}$$

The rate of increase in fitness is strongly affected by the physical environment. The simple presence of liquid water is not sufficient for the rapid evolution of multicellular organisms. Other "nutrients," which in optimal quantities support diverse ecosystems such as rain forests (Figure 14, "'Eden' planet"), are also necessary and these "nutrients" may only be present in biologically significant quantities for about 1.5 billion years of the total 10 billion year lifespan of the Earth during which time abundant oxygen and carbon dioxide will be present in the planetary atmosphere. Beyond this interval, only "artificial Edens" will be sustainable on the planet.

The interplay between physical and biological processes suggests that the appearance of dinosaur-like creatures was probably more or less expectable in the history of life on Earth. These creatures can be regarded as pertaining to a "medieval" or a middle stage in the evolution of life, as the name of the Mesozoic Era during which they lived suggests. However, relatively high levels of activity and

behavioural flexibility were as important then in defining fitness as are relatively high levels of activity ("work") and behavioural flexibility ("thought") in defining human fitness today.

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The Recapitation of *Apatosaurus*

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INTRODUCTION

In 1915 the Carnegie Museum of Natural History's magnificent skeleton of the sauropod dinosaur *Apatosaurus louisae*, discovered in 1909 at what is now Dinosaur National Monument in northeastern Utah, took its place alongside the equally impressive skeleton of *Diplodocus carnegii* in the Hall of Dinosaurs. At that time and for the next 17 years, however, it stood conspicuously headless. It was not until December of 1932 that the skeleton was completed, and then with the wrong head—a *Camarasaurus* skull. How this came about and how the error was corrected requires the untangling of a long series of events that began with the first discoveries and descriptions of the giant sauropod dinosaurs of North America over a century ago.

EARLY HISTORY

The year 1877 marks the beginning of what was undoubtedly one of the most notable periods in the field of vertebrate paleontology, the discoveries on a large scale of the first gigantic, quadrupedal, sauropod dinosaurs from the Upper Jurassic (about 150 million years ago) deposits of western North America. The limelight of these discoveries was shared simultaneously and almost exclusively by two of the most energetic and respected paleontologists of the time: Edward Drinker Cope of the Academy of Natural Sciences of Philadelphia, and Othniel Charles Marsh of Yale University. Unfortunately, both scientists were engaged in a bitter rivalry that lasted until their deaths at the end of the century and, although they can be credited with advancing paleontology at an unprecedented rate, their often short, hastily written scientific publications frequently resulted in confusion and misconceptions about the animals they described that lasted long after their deaths. The first description of *Apatosaurus* by Marsh (1877*b*) and of *Camarasaurus* by Cope (1877), both of which appeared over a century ago, were very brief and without any illustrations. In their
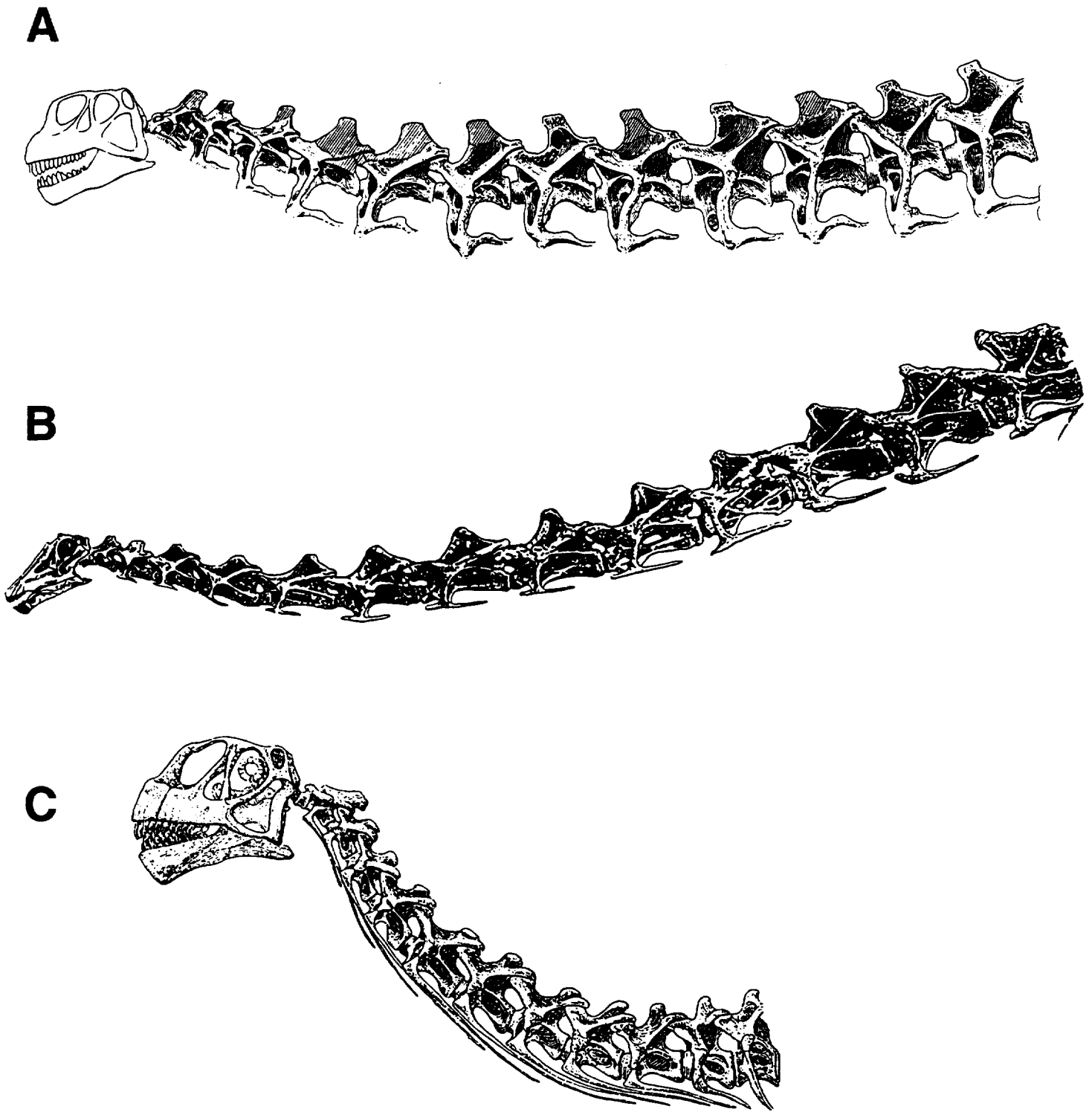
Figure 1. Skeletal reconstructions of A, *Apatosaurus louisae* CM 3018 shown restored with *Camarasaurus*-like skull (after Gilmore, 1936), B, *Diplodocus carnegiei* (after Holland, 1906), and C, *Camarasaurus lentus* CM 11338 (after Gilmore, 1925). Scales: A, B = x ⅟₃₀ . C = x ⅟₁₀ .

zeal to describe the first large sauropod of North America, both Marsh and Cope rushed into publication with descriptions of the first few bones they received from their collectors in the field, even though they knew that the greater parts of the skeletons were still being excavated.

During the next year and a half, as more material was collected and prepared, these descriptions were only slightly expanded, but neither animal received the attention it merited and thereafter they were essentially ignored. Adding to the confusion, at this time Marsh (1878*b*, 1879) also described two more sauropod dinosaurs, *Morosaurus* and *Brontosaurus*, both of which are now recognized as being the same animals as *Camarasaurus* and *Apatosaurus*, respectively. "*Morosaurus*" and "*Brontosaurus*" were based on good, more complete specimens and were described in detail and with many excellent illustrations. However, of the half dozen or more partial skeletons Marsh had identified as "*Morosaurus*", all were juveniles or subadults and were considerably smaller than the two large skeletons of "*Brontosaurus*" that he had. Because he did not recognize that "*Morosaurus*" was a juvenile *Camarasaurus*, he came to the erroneous conclusion that "*Morosaurus*" was a much smaller animal than "*Brontosaurus*". As a result, Marsh misidentified the few adult *Camarasaurus* specimens he had as "*Brontosaurus*" because of their large size. Further, Marsh and others had also recognized that the skeletons of *Apatosaurus* ("*Brontosaurus*") and, to a somewhat lesser extent, of *Camarasaurus* ("*Morosaurus*") are very robustly built and their hindlimbs are nearly indistinguishable (Fig. 1). On the other hand, it was also recognized that the skeleton of *Diplodocus*, another sauropod described by Marsh (1878*a*) and the third sauropod of this story, is very slender in build, and its hind limbs are easily identified (Fig. 1). Thus, it was mistakenly believed that the skeletons of *Apatosaurus* and *Camarasaurus* are much closer in overall structure than either is to *Diplodocus*. These errors in reasoning became firmly fixed in the literature with Marsh's reconstructions of "*Brontosaurus*" in 1883 and 1891, which were based on one of the most complete sauropod skeletons ever found.

His 1883 reconstruction was the first published for any North American sauropod. Although it was remarkably good in many ways, especially for its interpretation of sauropod posture (particularly the elephant-like stance with the slightly bent limbs directed beneath the shoulders and hips), it contained many inaccuracies that gave *Apatosaurus* a distinctly *Camarasaurus*-like appearance. As examples, for the missing forelimb and foot Marsh used a partial skeleton of a large *Camarasaurus* in which the elements are narrower and longer. The neck was shown as having 12 vertebrae, as in *Camarasaurus*, instead of the 15 known for *Apatosaurus*. The tail was restored short, as in *Camarasaurus*, since Marsh had no way of knowing that *Apatosaurus* had a long whip-lash tail that contained almost twice as many vertebrae as in *Camarasaurus*. However, the most serious error in this reconstruction was the skull. For that, Marsh used a large, incomplete *Camarasaurus* skull found in a quarry a considerable distance from the quarry with the *Apatosaurus* skeleton. This second quarry has
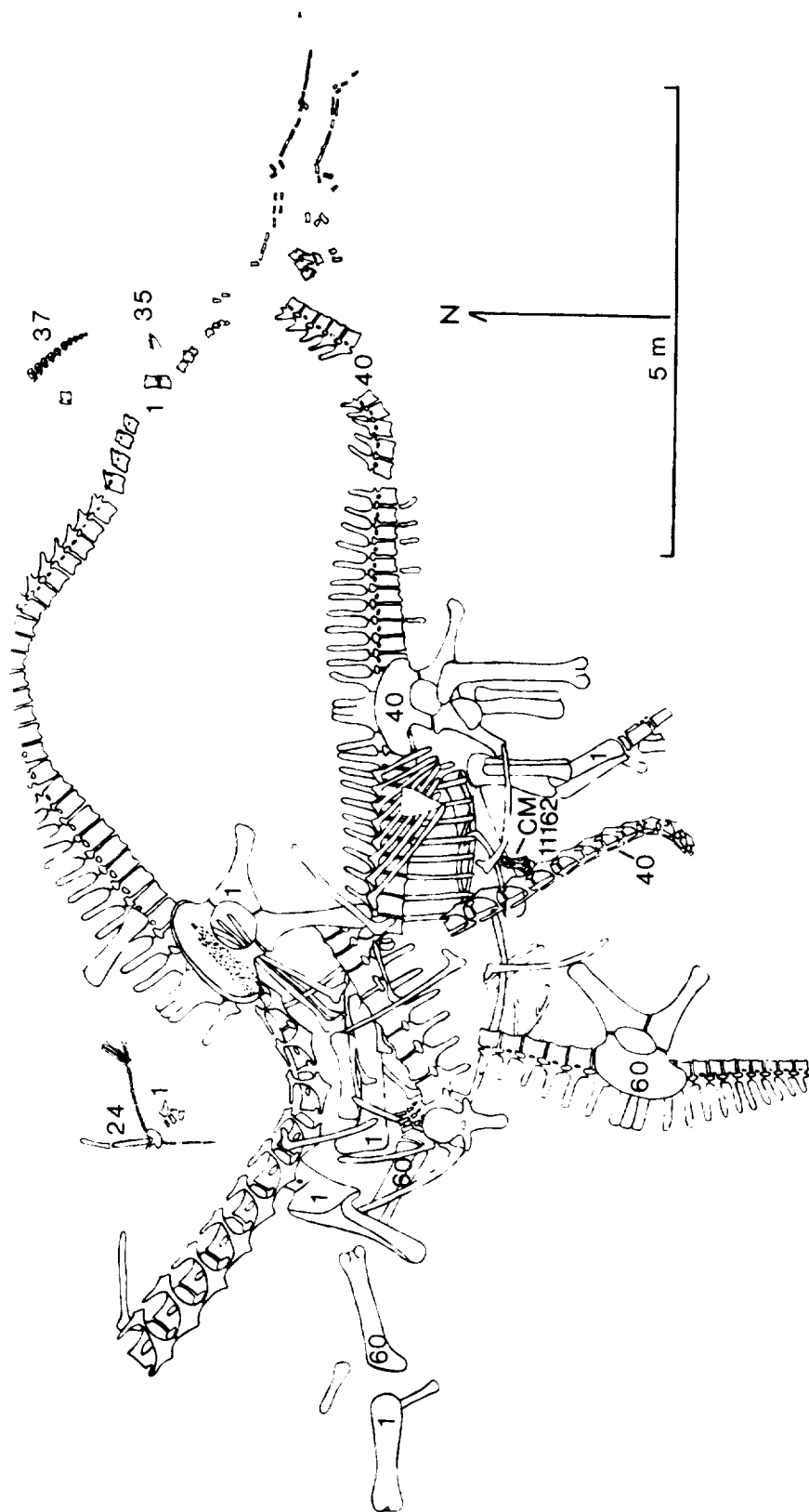
Figure 2.—Redrawn portion of Dinosaur National Monument quarry map on file at Carnegie Museum of Natural History showing the relative positions of sauropod dinosaurs removed by that institution and discussed in text. Field no. 1, holotypic postcranial skeleton of *Apatosaurus louisae* CM 3018 on exhibit at the Carnegie Museum of Natural History; field no. 40, postcranial skeleton of *Apatosaurus* now at the Los Angeles County Museum, California; CM 11162, skull very probably belonging to field no. 1 or possibly no. 40; field no. 60, postcranial skeleton of *Apatosaurus*; field no. 24, portion of postcranial skeleton of a juvenile *Apatosaurus* (CM 3390), field no. 37, series of cervical vertebrae; and field no. 35, anterior portion of small jaw with *Diplodocus*-like teeth, probably belonging to one individual of *Apatosaurus*.

yielded four *Camarasaurus* skeletons and other bones of that animal, but none of *Apatosaurus*. Marsh's revised 1891 reconstruction was in some ways less accurate than his first. Although he added a thirteenth vertebra to the neck, bringing it closer to the correct number of 15, he also increased the number of the trunk vertebrae from ten, the correct number, to 14. *Camarasaurus* has 12. In this revised reconstruction a second, somewhat more complete, *Camarasaurus* skull was used; however, this skull was found in a quarry some 400 miles from the skeleton. This distant quarry did contain *Apatosaurus* bones, but also those of at least four other kinds of sauropods, and the skull itself was not associated with any other bones.

Had Marsh realized that "*Morosaurus*" grew to the same size as "*Brontosaurus*" he might not have used the large *Camarasaurus* skulls or forelimb and foot in his reconstructions of "*Brontosaurus*". Yet, these specimens are not especially large when compared to the *Camarasaurus* specimen described by Cope in 1877. The fact that Marsh never indicated his use of secondary specimens, their selection seemingly made on purely speculative grounds, to complete his reconstructions of "*Brontosaurus*" undoubtedly helped to perpetuate many of the misconceptions about the anatomy of *Apatosaurus*. As if the confusion created by Marsh's reconstructions was not enough, in 1898 Henry Fairfield Osborn of the American Museum of Natural History, by then the most dominant paleontologist of the time, described a "*Brontosaurus*" skeleton as *Camarasaurus*, apparently believing the two animals were the same.

APATOSAURUS SPECIMENS FROM CARNEGIE QUARRY

The single most important event with regard to this story was the discovery in 1909 by Earl Douglass of the Carnegie Museum of Natural History of the well-known, richly fossiliferous dinosaur quarry at Dinosaur National Monument, then known as the Carnegie quarry. The first specimen he discovered and excavated, designated field no. 1, was important not only in being the most complete *Apatosaurus* skeleton ever found, but in having a large skull closely associated with it (Fig. 2). Lying beside field no. 1 was a second, almost as complete but slightly smaller, skeleton of *Apatosaurus*, field no. 40. Alongside the neck of no. 40 and about 12 feet from the end of the neck of no. 1 was a large *Diplodocus*-like skull without the lower jaws which was given the Carnegie Museum of Natural History catalogue number CM 11162 (Fig. 2). Although the rear part of a medium-sized *Apatosaurus* skeleton lay only about nine feet from the skull, their relative size difference eliminated any possibility that they were part of the same individual. William Jacob Holland, then Director of the Carnegie Museum of Natural History, and Earl Douglass, field collector in charge of quarrying operations at the Carnegie quarry, immediately recognized that the skull (Figs. 3, 4) must be that of *Apatosaurus*. However, since this skull resembled that of *Diplodocus* (Fig. 5A), it contradicted the long and widely accepted belief that *Apatosaurus* had a skull
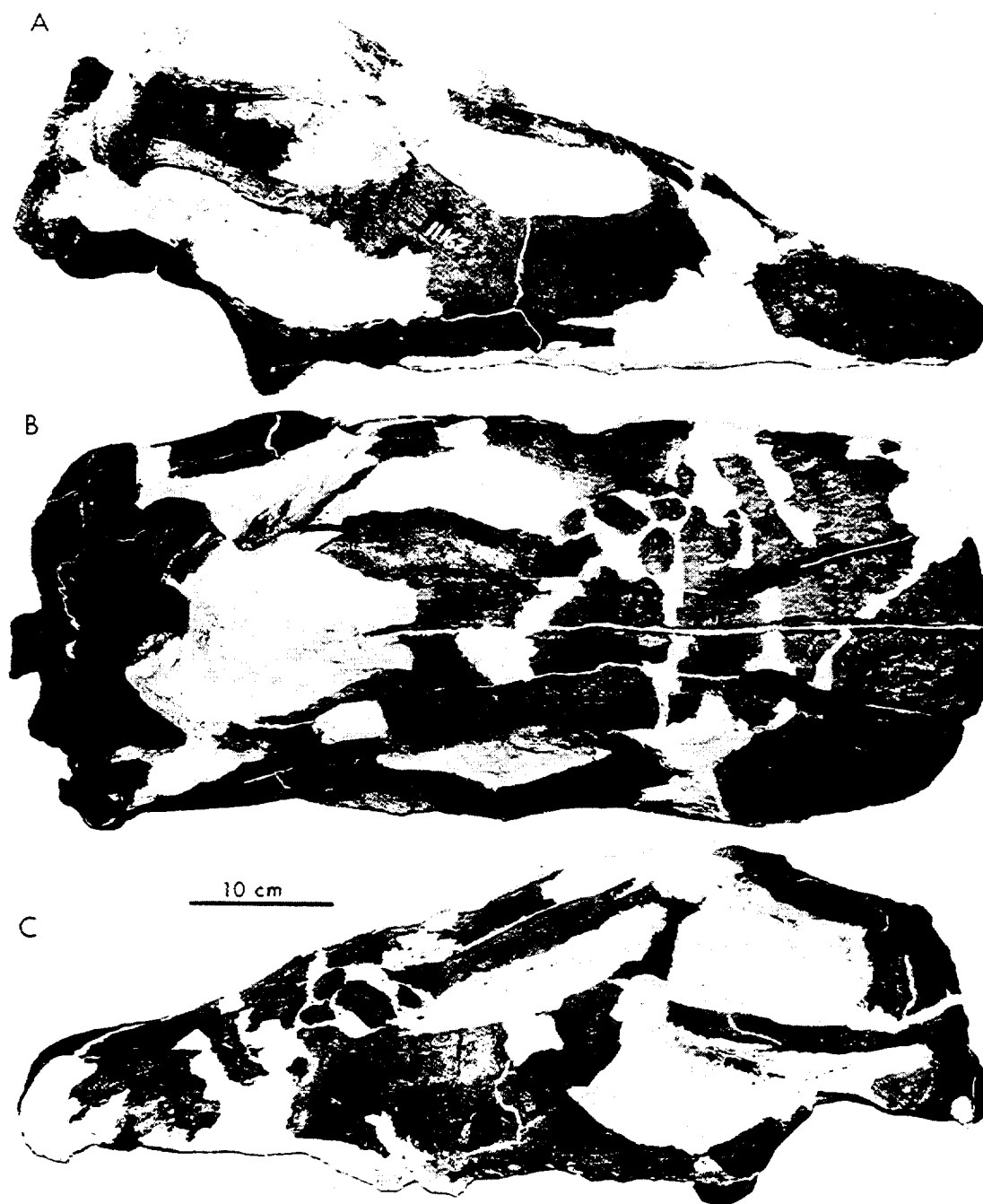
Figure 3.—Probable *Apatosaurus* skull CM 11162 from Dinosaur National Monument quarry. A, right lateral; B, dorsal; and C, left lateral views. Functional teeth have been lost, but pencil-like replacement teeth of right maxilla are partially exposed due to loss of surface bone.
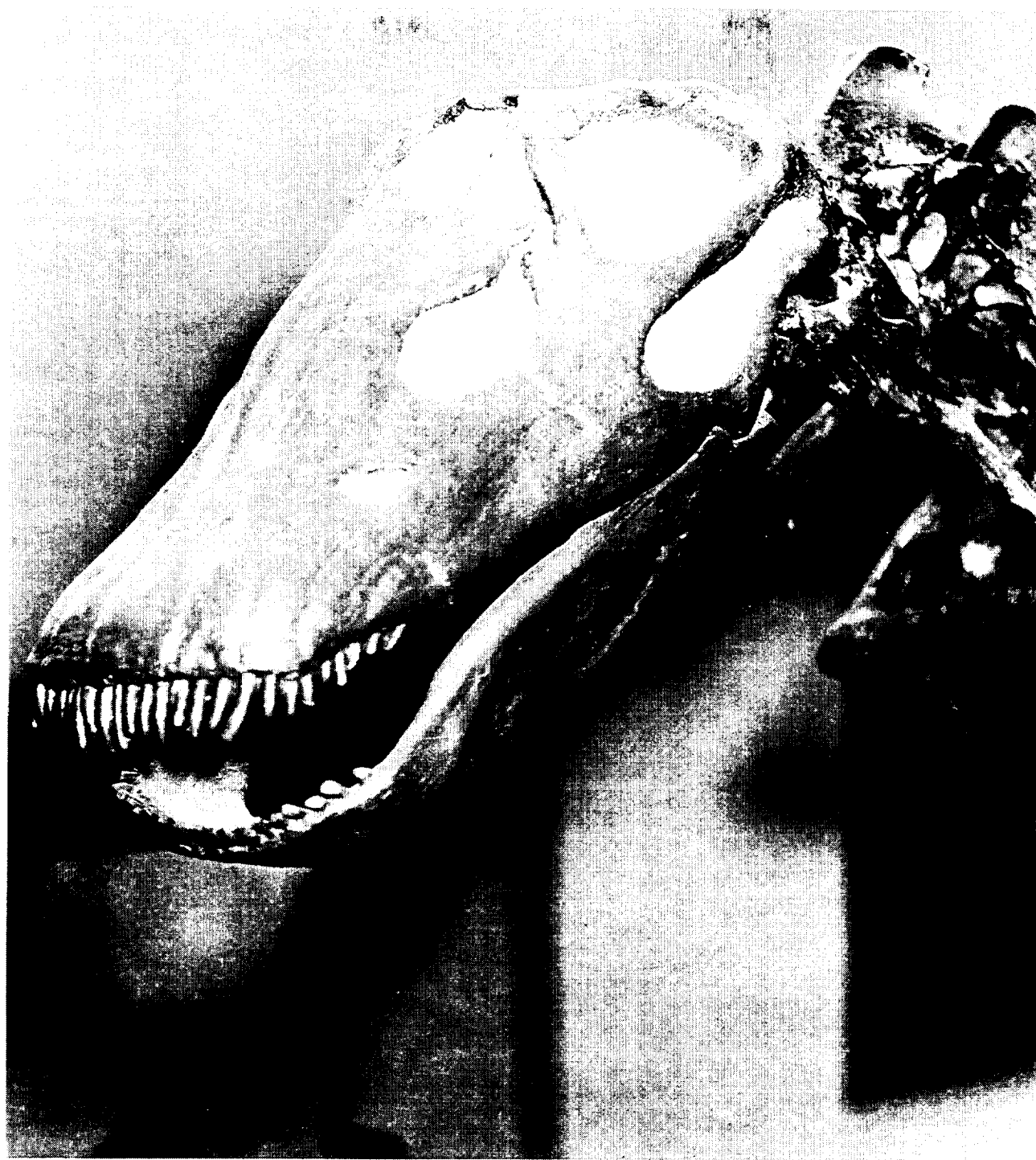
Figure 4.—Cast of restored probable *Apatosaurus* skull CM 11162 shown mounted on *A. louisae* skeleton CM 3018 at Carnegie Museum of Natural History.

A

B
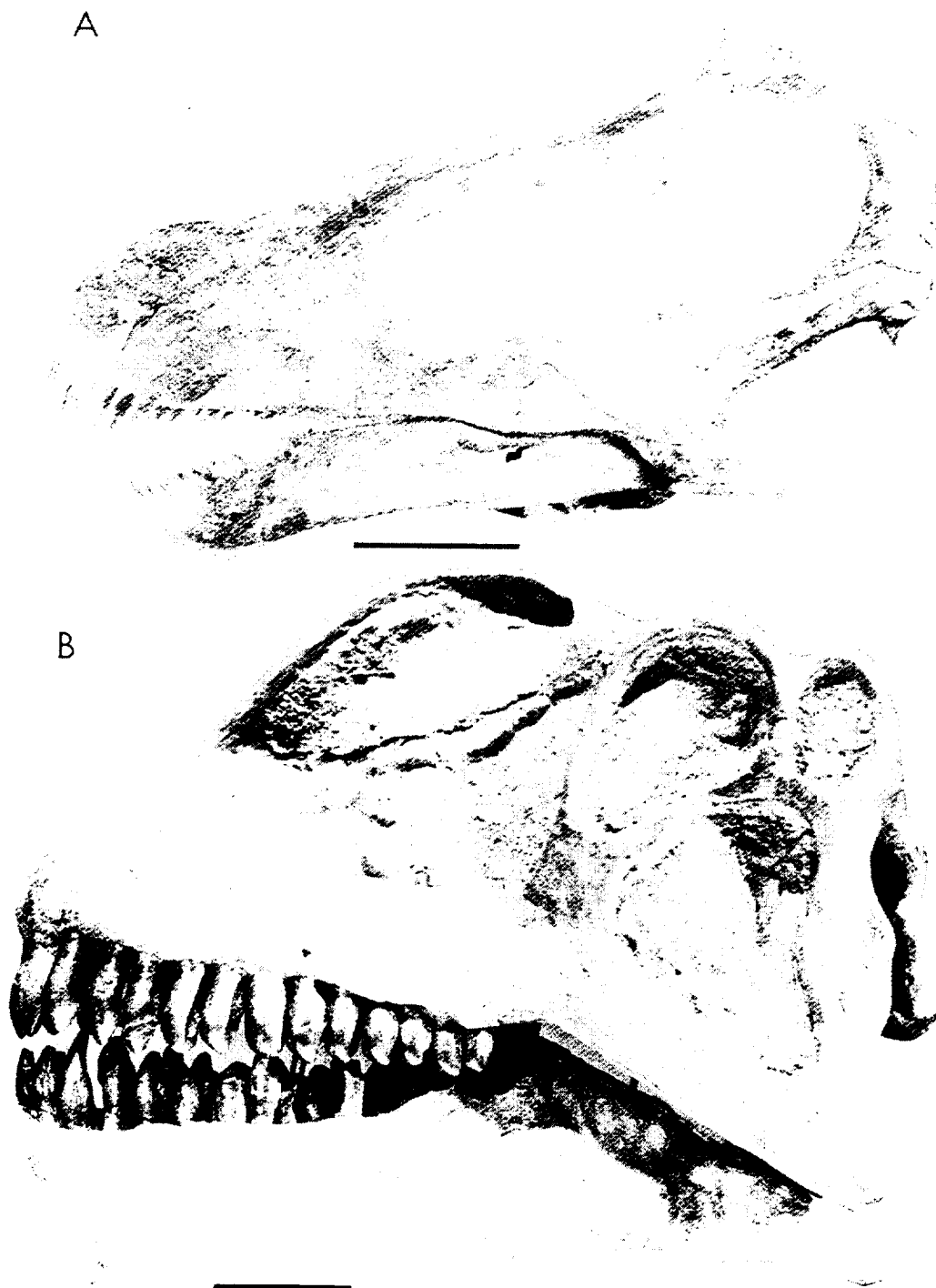
Figure 5.—Skulls of A, *Diplodocus longus* CM 3452; and B, *Camarasaurus lentus* CM 12020 from Dinosaur National Monument in left lateral view. Scales = 10 m.

resembling that of *Camarasaurus* (Fig. 5B). In a letter to Douglass dated December 3, 1914, Holland wrote,

> I however have the impression, as I have already stated to you in conversation, that other genera and species had skulls very much like Diplodocus, and I should not be at all surprised to find in the end that Brontosaurus and Apatosaurus and all the rest of them really belonged to the [Family] Diplodocidae, when the structure of their skull comes to be known, and that the separation into families of certain of these animals is in error. This of course is mere surmise and is not capable of verification, but as you know things point in that direction.

> Professor Marsh's material upon which he based his restoration of the skull of his so-called Brontosaurus was derived from two sources. The first was a fragment found by W. H. Reed fifteen hundred feet away from the spot where he excavated Marsh's type of Brontosaurus excelsus. It was found in the talus of Como Bluff. The remainder of the material upon which Marsh based his conclusions was obtained at Felch's Canon City quarry, which is hundreds of miles from Como Bluff. The latter material is in the U. S. National Museum and has never been published upon except as utilized by Marsh in bringing about his restoration. The association of this skull material with what Marsh denominates the type of Brontosaurus is wholly arbitrary, and I doubt its correctness, as I have repeatedly told you. ...I...hope you will send us by freight such material as you may have succeeded in recovering which bears closely upon the problem of the skull which we are at present discussing.

In 1915 Holland briefly described the postcranial skeleton of field no. 1, given the catalogue number CM 3018, as a new species, *Apatosaurus louisae*. Most significantly, on the basis of the skull associated with it, Holland also challenged Marsh's use of *Camarasaurus*-like skulls in his 1883 and 1891 reconstructions of *"Brontosaurus"*. Noting the close proximity of the skull CM 11162 to the skeleton CM 3018, their position in the same layer, and the exact fit of the skull with the first neck vertebra of CM 3018, Holland concluded that the *Diplodocus*-like skull represented the true skull of *Apatosaurus*. He stated (p. 274) that

> Had nothing in the past been written in reference to the structure of the skull of *Brontosaurus* the conclusion would naturally and almost inevitably have been reached that this skull belongs to the skeleton the remainder of which has been recovered.

But this new evidence on the true nature of the skull of *Apatosaurus* never gained serious consideration among paleontologists, and when the skeleton of *Apatosaurus louisae* was mounted at Carnegie Museum of Natural History, Holland refrained from

using the skull found with it. This headless state apparently reflected an unwillingness of Holland to oppose fully the opinions of his paleontological colleagues. The only clue we have to explain Holland's reluctance is his remark (1915:277) that "My good friend, Dr. Osborn, has in a bantering mood 'dared' me to mount the head...." And so *Apatosaurus* continued to be restored in journals, textbooks, museum exhibits, and cartoons as having a *Camarasaurus*-like skull. Holland retired on July 1, 1922, and became Director Emeritus of the Museum and Curator Emeritus of Paleontology but continued to work on a description of the osteology of *Apatosaurus* until his death on December 13, 1932. *Apatosaurus louisae* continued to stand headless in the Hall of Dinosaurs. And the same month that Holland died the Carnegie Museum of Natural History decided, probably at the persuasion of the highly influential Charles W. Gilmore of the United States National Museum (and a former field employee of Carnegie Museum of Natural History), to complete the mount with a cast of a large *Camarasaurus* skull that had been found a considerable distance from the skeleton at Dinosaur National Monument. This skull and the greater part of a postcranial skeleton of an adult *Camarasaurus* were collected together under the same field number and later both received the same catalogue number (CM 11393). There is no doubt that the skull and postcranial skeleton belong to the same individual and, further, no *Apatosaurus* material was found nearby to suggest otherwise. When the *Camarasaurus* skull was placed on *Apatosaurus louisae* it was recatalogued CM 12020, an action of questionable propriety. *Apatosaurus* no longer stood headless. Thus, the most dramatic vestige of Holland's important argument was eliminated and seemingly quickly forgotten.

In 1936 additional opposition to Holland's argument appeared when the Museum published a detailed description by Charles Gilmore of the postcranial skeleton of *Apatosaurus louisae*. Seemingly the force was taken out of Holland's argument by Gilmore's contention that the large *Diplodocus*-like skull purported to have been found with this skeleton had actually been confused with a much smaller *Diplodocus* skull, CM 11161, found closely associated with a medium-sized *Apatosaurus* specimen, field no. 160 (CM 3378), isolated at the far western end of the quarry. If this was the case, as pointed out by Gilmore, the skull CM 11161 was too small to have belonged to either *Apatosaurus louisae* postcranial skeleton no. 1 or no. 40, whereas the first skull, CM 11162, is far too big to have belonged to the skeleton of no. 160 (CM 3378). Gilmore made his assertion on the basis of conversations with J. Leroy Kay, at that time Assistant-in-Charge of Vertebrate Paleontology at Carnegie Museum of Natural History, who, beginning in 1915, had been a workman at the quarry. Why Kay suggested that the two skulls had been interchanged is unclear, since he was not involved in collecting them. That Holland was correct in the quarry positions of the two skulls has been positively documented by letters from Douglass to Holland. Concerning the discovery of the skull during the excavations of the *Apatosaurus* postcranial skeletons nos. 1 and 40 (Fig. 2) Douglass wrote to Holland on November 16, 1910, that "It seems pretty large to me—about 26 inches in length.... The mandible is not with the skull but may be near." Both the length and

the absence of the lower jaw clearly identify this skull as CM 11162. In a second letter dated November 29, 1912, he wrote, "Our work has of late been principally in the West Extension of the quarry.... One skeleton, No. 160 [CM 3378] is of especial interest.... Yesterday—Thanksgiving Day—I found a skull complete, with lower jaw nearly or quite in place...under the anterior portion of the tail." There can be no doubt that the latter skull is CM 11161.

What started out as a working hypothesis, that *Apatosaurus* and *Camarasaurus* are similar in overall structure and most likely had similar types of skulls, apparently became so entrenched in the literature and in the thinking of paleontologists that it ended up as a loafing hypothesis. With Gilmore's description of *Apatosaurus* in 1936 enough information had accumulated about the Jurassic sauropods of North America that an objective reconsideration of Holland's claim that *Apatosaurus* possessed a *Diplodocus*-like skull not only would have been timely, but might have swung opinion in Holland's favor. The skeletons of the three principal characters of this scenario, *Apatosaurus*, *Camarasaurus*, and *Diplodocus*, were now known in great detail, save the head of *Apatosaurus*, and even a cursory comparison of their postcranial skeletons (Fig. 1) would have revealed that *Apatosaurus* is not only quite distinct from *Camarasaurus*, but shares a great number of significant features with *Diplodocus*. By this time also it had been demonstrated that the names "*Morosaurus*" and "*Brontosaurus*" were merely synonyms of *Camarasaurus* and *Apatosaurus*, and they no longer clouded the picture. Therefore, if given the choice between a *Diplodocus*-like or a *Camarasaurus*-like skull for *Apatosaurus* and knowing nothing more than what the postcranial skeletons of these three animals look like, the obvious and unavoidable selection would surely have to be a *Diplodocus*-like skull. The soundness of this logic is reinforced if one takes into account Holland's disclosure of the source of the *Camarasaurus* skulls used by Marsh in his reconstructions of *Apatosaurus* and that there never existed any direct evidence to support such an association.

A Second Probable *Apatosaurus* Skull

There is now known a second, partial *Diplodocus*-like skull that most likely belongs to *Apatosaurus*; it also has had a long and extremely complicated history. In 1877 Marsh received from his collectors a partial sauropod skull as part of a large shipment that included specimens from three different quarries near Morrison, Colorado, nos. 1, 8, and 10. Apparently the importance of the skull was not realized at the time it was uncrated, since the specimen was not marked as to which quarry it was found in. However, circumstances leave little doubt that it had to have come from either quarry no. 1 or, more likely, quarry no. 10. Quarry no. 1 yielded a large, very incomplete sauropod sacrum, described by Marsh (1877a) as *Atlantosaurus montanus*, and *Camarasaurus* vertebrae. On the other hand, the total yield from quarry no. 10 was two very large postcranial skeletons of *Apatosaurus ajax*. One was catalogued as Yale Peabody Museum specimen YPM 1860 and is the specimen on

which Marsh (1877*b*) based his original description of *Apatosaurus*, whereas the other was catalogued as YPM 1840 and was originally described by Marsh (1878*a*) as representing a new species of *Atlantosaurus*, *A. immanis*, but is now recognized as a second specimen of *A. ajax*. Because, for reasons unknown to us, Marsh (1896) figured the skull as *Atlantosaurus montanus*, it would appear that he believed it to be from quarry no. 1, since this species is known otherwise only by a sacrum from that quarry. As it turns out, however, the sacrum is not only too fragmentary to assign to either *Apatosaurus* or *Camarasaurus*, but also to any known sauropod family. In sorting out the specimens from Morrison, Colorado, S. W. Williston, a preparator of Marsh's who later became a highly respected paleontologist in his own right, assigned the skull to the "*Atlantosaurus immanis*" (=*A. ajax*) specimen YPM 1840, indicating he believed it to be from quarry no. 10. The partial skull now bears the catalogue number YPM 1860, but we do not know when, by whom, or on what basis it was given this number. It is possible that either Williston or Marsh may have received more precise locality information for the skull well after it arrived at the Yale Peabody Museum and that this was never recorded in the catalogues. At any rate, in 1958 Theodore E. White, then paleontologist at Dinosaur National Monument, quite reasonably assumed that the catalogue number YPM 1860 on the skull meant that it belonged to the postcranial skeleton of *Apatosaurus* YPM 1860 and that Marsh had erred in describing it as *Atlantosaurus montanus*. Further, White thought the skull closely resembled that of *Camarasaurus* and therefore provided evidence of a close relationship between *Apatosaurus* and *Camarasaurus*. White's observations could have sounded the final death knell to Holland's assertion. However, a more recent study (McIntosh and Berman, 1975) of the Morrison skull revealed that, in contrast to White's claim, it is *Diplodocus*-like. Also of great importance to this debate is a pair of large, identical, quadrate bones (the skull bone on which the lower jaw hinges) definitely known to have been collected from quarry no. 10 at Morrison, which yielded two excellent skeletons of *Apatosaurus* and no remains of any other sauropod. The quadrates are essentially indistinguishable from those of *Diplodocus* and, in turn, are quite distinct from those of *Camarasaurus*. On the basis of size and color there is a very strong possibility that the quadrate bones and the partial skull not only belong to the same individual, but to the *Apatosaurus ajax* postcranial skeleton YPM 1860 (McIntosh and Berman, 1975; Berman and McIntosh, 1978). It is surprising that White (1958) apparently was not aware of the pair of quadrates, since, if he had examined them, he surely would have recognized their *Diplodocus*-like structure and so might also have noticed the *Diplodocus*-like nature of the skull.

A FINAL ANALYSIS LEADS TO SKULL CHANGE

Although not absolutely conclusive, the evidence strongly supports Holland's argument that the skull of *Apatosaurus* looked like that of *Diplodocus*. If Marsh had not arbitrarily assigned isolated *Camarasaurus* skulls to "*Brontosaurus*" there can be little doubt that the large *Diplodocus*-like skull (Figs. 3, 4) found at Dinosaur

National Monument would have been readily and widely accepted as the true skull of *Apatosaurus*. Holland recognized this, stating (1915:275),

> It is plain...that Professor Marsh associated the skulls, which he had studied, with the remains of *Brontosaurus* as a result of a process of ratiocination, rather than as the result of ocular evidence that the skull actually belonged with the skeleton.

Concluding, Holland believed that no

> man is in a position to declare with positive assurance that the skull heretofore attributed to the genus *Brontosaurus* actually belonged to it.... Were it not, as I have already intimated, for Professor Marsh's action, the writer would be tempted to declare that the skull of *Brontosaurus* was not very different from that of *Diplodocus* in its main structural features in view of the fact that the skull in his possession lay only twelve feet from the cervical vertebrae and other skeletal remains [of *Apatosaurus louisae*] before him.

The long-neglected controversy raised by Holland (1915) was not reopened again until over a half century later (McIntosh and Berman, 1975; Berman and McIntosh, 1978). With a new analysis of the old evidence, it has been shown that there now is little doubt that Holland was correct. Even the most casual observer will be struck by the obvious differences between the two types of skull: the skull of *Camarasaurus* (Fig. 5B) is short-snouted and high-crowned, stoutly constructed, and possesses large, spatulate-shaped teeth, whereas, in contrast, the nearly indistinguishable skulls of *Apatosaurus* and *Diplodocus* (Figs. 3, 4, 5A) are low, long-snouted, and delicately constructed with narrow, pencil-like teeth.

With this realization, on October 16, 1979, the *Apatosaurus louisae* skeleton of the Carnegie Museum of Natural History was given a new look with the replacement of its *Camarasaurus* skull with a restored replica of the *Diplodocus*-like skull discovered with it at Dinosaur National Monument (Fig. 6)—an event that surely would have greatly pleased W. J. Holland. In the years following this event the skeletons of *Apatosaurus* on exhibit at the University of Wyoming, the Field Museum of Natural History, the Yale Peabody Museum of Natural History (home of the first mounted *Apatosaurus* skeleton, done under the direction of Marsh), and the American Museum of Natural History have also been changed to portray them as possessing a *Diplodocus*-like skull, using casts of the restored probable *Apatosaurus* skull CM 11162 of the Carnegie Museum of Natural History.

SIGNIFICANCE OF SKULL CHANGE

Now that *Apatosaurus* has been restored with a dramatically different type of head not only must our views on its relationships to the other sauropods be drastically revised, but our speculations—often quite controversial—on its life habits. In addition

Figure 6.—Cast of restored probable *Apatosaurus* skull CM 11162 being installed on *A. louisae* skeleton CM 3018 at Carnegie Museum of Natural History.

to the recognition that the postcranial skeletons of *Apatosaurus* and *Diplodocus* share many significant features that give them a much closer resemblance to one another than either exhibits with *Camarasaurus*, the same can now be said to be even much truer regarding their skulls. The skulls of *Apatosaurus* and *Diplodocus* differ from one another in only subtle proportions or minor structural details (Berman and McIntosh, 1978) and are quite distinct from that of *Camarasaurus*. With this new information on the anatomy of *Apatosaurus*, it becomes apparent that it is not closely related to *Camarasaurus*, but rather is more appropriately united with *Diplodocus* as a member of the family Diplodocidae. With its former, short-snouted, *Camarasaurus*-like skull with broad, spatulate-like teeth *Apatosaurus* was most commonly envisioned as a dry-land dweller capable of browsing on rather coarse vegetation at considerable heights. With its newly acquired *Diplodocus*-like skull *Apatosaurus* will probably be pictured by most scientists as a herbivorous inhabitant of swamps and lagoons. The fragile forward-slanting, pencil-like teeth concentrated at the front of its relatively long jaws indicate a specialized diet, or at least a diet quite different from that of *Camarasaurus*. It is not unlikely that the dentition of *Apatosaurus*, as well as that of *Diplodocus*, was adapted for cropping the soft, succulent, bottom vegetation of a shallow-water habitat. Supporting this view is the fact that with its elongated snout and nostrils positioned high atop the skull, *Apatosaurus* could graze with its head almost completely submerged, yet continue to breathe.

ACKNOWLEDGMENTS

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Amateur and Commercial Collecting in Paleontology

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"...SPEAK TO THE EARTH, AND LET IT TEACH YOU."
(Job 12:8 NASB)

Ambitious collectors have been gathering fossils for centuries and should be allowed to continue. A glimpse at fossil collecting through history gives us an idea of how paleontology affects people. A Roman ruler, Gauis Caesar, better known as Caligula, did some field work in paleontology. Caligula was most likely mad. One of the common proofs pulled from history affirming his madness is the fact that he made his horse a councilman advisor to the senate. There are so many stories of the perverted life Caligula led, it is likely the term "caliginous," which describes dark and gloomy aspects, came from his name.

Around A.D. 38, Gauis Caesar invaded Britain and ordered his soldiers to fill their treasure chests with ammonites (a fossil chambered nautilus) that littered the coast. In a speech after his triumphant return to Rome, he announced he had "conquered Britain because he had conquered [its] past." It is easy to laugh at the mad Caesar and the preposterous idea that he had conquered a civilization by stealing a few Jurassic mollusks. Equating the two is a stretch of logic...maybe madness. Ironically, this bit of faulty logic is being used again centuries later.

The ammonites collected by Caligula were probably a species of *Hildoceras*, a common example found in the Lias shale of the Jurassic period and named for St. Hilda of Whitby, Yorkshire. According to a legend revived by Sir Walter Scott in his poem, *Marmion*, St. Hilda was responsible for the existence of ammonites through her work in A.D. 638.

"They told how, in their convent cell/ A Saxon princess once did dwell, the lovely Edelfield/ And how of thousand snakes, each one was changed into a coil of stone/ When Holy Hilda prayed/ Themselves within their holy bound/ Their stoney folds had often found...

Even today the town of Whitby has three ammonites in its coat of arms. The ruined St. Hilda's Abbey became part of another legend when the British writer, Bram Stoker, used it for the model of Dracula's castle in his famous work.

The Lias shale ammonites and vertebrate remains were collected and sold for centuries. In Lyme Regis, Dorset, a carpenter and his daughter sold the fossils they found to supplement his income. When Mary Anning's father died she was only ten years old and continued to provide for herself the only way she knew. The little girl's life became the basis for the famous tongue twister, "She sells sea shells by the sea shore."

Mary Anning's gift to society goes beyond this little ditty. She collected and sold to institutions the first articulated ichthyosaur (1810) and plesiosaur (1823), as well as the first British pterosaur (1828). She was lifelong friends with Henry de la Beche, William Conybeare, and William Buckland, the fathers of paleontology. These men endorsed her work and referred to her as "the most eminent female fossilist."

In the United States, some of the earliest records of commercial collecting are from the plains tribes of the Arapahoe and the Cheyenne. They collected and traded weathered sections of *Baculites* (another "straight-shelled" fossil ammonite). These eroded fossil fragments were called "Buffalo Stones," because they resemble the animal that was the tribe's life support system.

The famous Cretaceous dinosaur beds of the western interior were tapped almost 200 years ago. William Clark, of the famous exploring duo, Lewis and Clark, found what was almost certainly a dinosaur bone in his travels along the Missouri River. An entry in his journal for Friday, July 25, 1806, describes waiting for his men to retrieve two bighorn sheep he had shot: "I employed my self in getting pieces of the rib of a fish which was Semented[sic] within the face of the rock this rib is about 3 inches in Secumpherence[sic] about the middle, it is 3 feet[in length] tho a part of the end appears to be broken off..."

Because Clark was in a portion of the Hell Creek Formation, a Late Cretaceous stratum famous for dinosaurs, and based on the dimensions he describes, it is doubtful that the "fish" was a fish but highly probable that what Clark had discovered was a dinosaur bone. Unfortunately, the actual fossil was not preserved, so no one will ever know.

In 1847, Dr. Hiram A. Prout of St. Louis described a fragment of the lower jaw of a titanothere in the *American Journal of Science*, calling it a "Paleotherium." Later the same year, Dr. Joseph Leidy described a well preserved camel skull in the *Proceedings of the Academy of Natural Sciences of Philadelphia*. Both specimens had been originally collected by fur trappers harvesting natural resources somewhere in the vicinity of what are now the towns of Wall and Scenic, South Dakota.

These discoveries initiated an era of scientific and commercial interest in fossils and sparked a rush of collecting on the western plains. Many large eastern universities and museums began sending collecting teams into the field, in the hopes of garnering glory by being the first to discover important specimens.

Besides the competition between institutions, infamous personal rivalries developed among collectors. Most notable was the enmity between Edward Drinker Cope and his nemesis Othniel Charles Marsh. It began, according to one story, in 1868 when Professor Cope described the newly found *Elasmosaurus* skeleton and erroneously placed the animal's head on its tail. Marsh pointed out the mistake to Cope. Cope, being of what was called "fiery temperament," was humiliated and angry at his mistake. This event apparently caused enough friction between the two men to embitter them for decades. They remained enemies and fierce competitors for fossils, notoriety, and scientific accomplishments. Stories abound of their collecting teams waging battles with fists and rocks over particularly rich fossil beds. One apocryphal story has it that the term "coprolite," the scientific term for fossilized feces, was coined by Marsh in "honor" of his arch rival, Cope. This is not true, however, since the word was invented by William Buckland and Mary Anning in 1821, during their work on the Lias shale of England, years before Marsh and Cope were feuding.

Beyond the threat of opponents hijacking fossil beds and throwing rocks were the everyday dangers of life in the Wild West. No roads, unfamiliar and rugged surroundings, and uncertain animosity between Indians and whites made fossil collecting a true adventure. Fortunately, most encounters with the Indians were peaceful and even beneficial to the fossil collectors, with the Indians sometimes directing the collectors to outcroppings and specimens. The frontier often demanded creativity as well as physical stamina and luck in hunting fossil. On one occasion, Cope encountered a number of Indians and, after establishing that they were not going to

murder him, entertained his visitors (at their insistence) by popping his false teeth in and out of his mouth!

Cope sold most of his collection in 1895, the year after his daughter's wedding, to the American Museum of Natural History in New York. His collection of mammals from North America sold for approximately $32,000. This collection contained over 10,000 specimens consisting of 463 species. The remaining 3,000 specimens mentioned in his papers brought almost $29,000. Expensive as this seems it was dwarfed by Marsh's collection, which was valued at one million dollars.

A landmark discovery in paleontology occurred in 1908 when the famous commercial fossil hunter Charles H. Sternberg and his three sons discovered the first of two mummified hadrosaurs, complete with beautifully preserved skin, webbed "hands," and internal organs. The specimens are now on display at the American Museum in New York City. In *The Great Dinosaur Hunters and Their Discoveries*, Edwin Colbert describes George Sternberg's discoveries of the first hadrosaur in 1908. The four Sternbergs had been in the field collecting, with rather poor results. Their morale was low and so was their food supply. The elder Sternberg and his son Charles went into town to buy supplies, leaving the two brothers, George and Levi, at camp with nothing but potatoes to eat. While waiting for the supplies to arrive, they decided to dig out a duck-billed dinosaur, which George had found earlier, sticking out of a sandstone cliff. In an account told by George years later, he said: "Finally by the evening of the third day I had traced the skeleton to the breast bone, for it lay on its back with the ends of the ribs sticking up. There was nothing unusual about that. But when I had removed a rather large piece of sandstone rock from over the breast I found, much to my surprise, a perfect cast of a skin impression beautifully preserved. Imagine the feeling that crept over me when I realized that here for the first time a skeleton of a dinosaur had been discovered wrapped in its skin. That was a sleepless night for me. Had I missed my regular cup of coffee or eaten too many potatoes for supper?"

Besides the bones and shells of long-dead animals, my home state of South Dakota has yielded the petrified remains of ancient, extinct plants. The celebrated novelist and poet, Edgar Allan Poe, in a passage from *The Thousand-and-Second Tale of Scheherazade*, writes: "Leaving this island, we

came to another where the forests were of solid stone, and so hard that they shivered to pieces the finest-tempered axes with which we endeavored to cut them down." In Poe's footnotes concerning this passage, he describes three fossil forests, one of which he places "near the head waters of the Chayenne, or Chienne River, which has its source in the Black Hills of the Rocky chain."

The forest to which Poe refers once stood in south-western South Dakota on the western edge of the Black Hills. The past tense is used here with a certain degree of irony; not only did the living forests of cycads once occupy this location in the late Jurassic and Cretaceous times, but the fossilized cycad forest occupied the site of the Cycad National Monument, so named in 1922 and up to 1954. Even in 1922, the "park" designation was somewhat superfluous: it had been completely devoid of cycads since the late 1800s when all of the fossils were removed by looters.

And who were the perpetrators of this heinous rape of protected land and a priceless natural wonder? No less than those celebrated paleontological ruffians at the American Museum of Natural History in New York, who carted away some 50 specimens, their cohorts in crime, the then-directors of the South Dakota School of Mines, who stripped of another 50, and of course the granddaddy scientific hooligan of them all, Mr. Neil Peabody of the Peabody Museum, who hauled away no fewer than 700 specimens! It took a special spur of railroad track and an entire boxcar to move the greater part of South Dakota's petrified cycad fossils east, where they still reside. Thus, the cycad forest was finally, after countless years, truly defunct. But, I am joking when I call them looters because they were not. These museums were properly harvesting a resource that was ripe and would have spoiled if not gathered.

There is a blight on paleontology today. It is impossible to receive a Bachelor of Science degree in paleontology in the United States. (The last graduating class was the University of Texas, 1989). Graduate programs are being modified or dropped from universities. Museum gift shops are not selling fossils and when they do, as Bringham Young University's museum does, they are heavily criticized. Even the U.S. government is getting into the act with a proposed Senate Bill. The bill, misnamed "The Vertebrate Paleontological Resources Protection Act," protects nothing: the dynamics of nature are cruel to fossils and left alone they are destroyed by erosion.

By discouraging an interest in fossils these forces will cause paleontologists to become as extinct as their subjects. And it is happening now. My cousin, who teaches at the University of Arizona, confesses the only way he can get students into the field is to make it a required class. This echoes complaints I hear from many paleontologists. We will have 400 million acres of public land set aside with nobody to study them. Even today those 400 million acres are the responsibility of 800 or so scientists. That makes for a half million acres per individual. (The six members of my family find it difficult to manage properly the one thousand acres of fossil sites on the family ranch, a ratio of 166 acres per person.) Shakespeare would agree. "They are as sick that surfeit with too much as they that starve with nothing," observed the maid of an heiress in *The Merchant of Venice.*

With reduced government funds, museums and universities should be courting the mining and energy companies, commercial paleontological suppliers, and rock clubs. Many are, but there is a caliginous minority that has disdain for the commercial and hobby collectors. That fierce form of patriotism known as jingoism veils the jealousy of groups that call for retaining "American fossils for Americans," while a refusal to return foreign fossil specimens is seen as consistent.

The jingoes claim we are losing our heritage if a fossil is sold outside a political boundary. Also, they believe that once a specimen crosses a political border it is lost to science, an archaic idea in a day of opening borders, global airlines, overnight mail, fax machines, modern molding techniques, and 3-D imaging. Interestingly, most fossils have more in common with their relatives in foreign formations and museums than they do with our modern society; and most people from the western United States feel closer to the non-renewable artwork of Frederic Remington and Charles Russell (which are sold at auctions for huge sums of money) than to the dinosaurs that preceded them on land.

To call fossils a rare and non-renewable resource is quite simply wrong. This would mean most theories about the fossil record are no longer in effect and the mineralization process has ceased to be viable. It also ignores the magnitude of fossil strata in the world. On our family ranch we have outcrops of the Oligocene White River Badlands. Popular theory holds that the Oligocene ended 20 million years ago and about half of the White River Group that was deposited has eroded away. If the erosion process began immediately after deposition then we have another 20 million years of fossils to collect from this group of fossil beds. Even if fossils can be collected for only one tenth that time, this still yields

fossils for the next 2 million years from this formation alone! How can you call "rare" a resource that requires two to twenty million years to consume? By that time there should be a supply of new fossil from the interim years.

Because of the nature of the rock deposits, the White River Badlands usually cannot be quarried. However, a neighboring formation can. This is the Eocene Green River Formation in western Wyoming. The fossil fish quarries of Kemmerer, Wyoming, which tap into just a small segment of the formation, are estimated to contain three fossil fish for each person in the world. Even parts of the expansive Hell Creek Formation can be quarried. The commercial Ruth Mason Quarry, run by the Black Hills Institute of Geological Research in central South Dakota, may contain 3,000 individual duck-billed dinosaurs, and is typical of the bone beds freckling the western plains. Since the summer of 1990, at least eight *Tyrannosaurus rex* skeletons have been found, one in a suburb of Denver! That is almost as many as were found in the previous one hundred years.

The romance that draws us to these dinosaurs is the same emotion that blinds us to the logical and practical aspects of the science. Logically, there is no difference between a commercial cement operation mining limestone on public land in the Black Hills, where I live, and a commercial paleontological operation in the same quarry. One grinds the Permian fish in that limestone into cement and sells the powdered fossils for financial gain and to aid society's construction; the other, valuing the specimens as *lusus naturae,* a freak of nature, collects them intact and sells them for financial gain and to aid society's science. Current proposed legislation will address only the paleontological business in this quarry, ignoring the loss of the specimens to the cement mixer.

That phrase of "fossils for sale" is dyspepsia to some people. A price of $250,000 for a dinosaur skeleton is called outlandish by some scientists; claiming it places the dinosaur beyond the humble museum's budget. Yet they will plead for $250,000-$1,000,000 for an expedition budget to collect their own dinosaur. An acknowledged cost exists but the recipient is the suspect factor in the equation. When it becomes more important who is involved in the work rather than the fact the work is getting done then we have people that are serving themselves and not science. If someone becomes bitter and angry because another person accomplishes a feat, then that emotion is based in jealousy. It is possible at this point they stop being scientists and become egotists. Such persons have not advanced further than Cope and Marsh,

standing on a hill in Wyoming throwing rocks at each other.

Anecdotal accounts of commercial collectors poaching on public land and using poor techniques on private land are exceptions. So too are the stories of museums and universities that lose field notes, drop and destroy display specimens, and collect on private land without permission. You can prove anything through example. The difference is the credibility of the accuser; especially if one has every advantage of education, wealth, and notoriety. Shakespeare's King Lear states it best: "Through tattered clothes small vices do appear; robes and furred gowns hide all. Plate sin with gold..."

Many of the fossils on display in museums around the world are the result of amateur and commercial collectors. Many, if not most, of the fossils on display here for "Dino-Fest" are from commercial collectors. Please, help be a part of paleontology by becoming involved with the commercial and amateur collectors here and around the world. You can do this by joining local clubs and global organizations. Also, you can learn more by visiting rock shops,

"That which has been is that which will be/ And that which has been done is that which will be done/ So there is nothing new under the sun." (Ecclesiates 1:9 NASB)

Society progresses at glacial speed and that thin veneer we call "civilization," at times, becomes transparent. Modern Caligulas equate sharing fossils to captivity. The faulty logic of not allowing greater freedom in the exchange of information is hurting our society and is just as mad today as it was in the day of Gauis Caesar.

FOSSILS AS A RESOURCE
COMPARISON

	Water	Range	Timber	Oil	Archeology	Paleontology
Commodity	NO	NO	YES	YES	NO	NO
Consumed (changed)	YES	YES	YES	YES	NO	NO
Renewable Temporal	YES 1	YES	YES	NO	NO	NO
Renewable Geological	YES	YES	YES	NO 2	NO/YES 4	YES
Perishable	YES	YES 3	YES	NO	YES 5	YES 6
Value Types	Life Sustain	Life Sustain	Indust. Life Sustain	Energy Indust	Academic Aesthetic	Academic Aesthetic Scientific
Regulated	YES	YES	YES	YES	YES	NO

1 Where resource comsumption is less than the recharge rate
2 Not renewable at the rate of consumption
3 Unsumed range contributes to soil nutrition
4 In some repect, the trash of our present civilization
   will become the arifacts of the future
5 Not all archeological resources are perishable
6 Once exposed by weather fossils are destroyed

Dinosaur Studies
in the
Pre-K Through Junior High Curriculum

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INTRODUCTION

I have always loved dinosaurs, and I feel fortunate to be able to teach teachers and students about dinosaurs as part of my profession; and yes, my name is really Dinah. Every year for the past 10 years, I have worked with thousands of teachers and students across the United States. During this time, I have made a startling discovery not mentioned in any of the classic human growth and development textbooks. I have found that most Americans pass through the following developmental stages, based upon dinosaurs:

Stage One: Aware of Dinosaurs (2-3 years of age).
Stage Two: Fascinated by Dinosaurs (4-5 years of age).
Stage Three: Obsessed with Dinosaurs (normally around the age of 5).
Stage Four: Dinosaur Expert (by age 6 or 7).
Stage Five: Continues to show an interest in studying dinosaurs in depth if the study is initiated by someone else (ages 8 to 10).
Stage Six: Still interested in viewing dinosaur exhibits and investigating a new dinosaur discovery (ages 11 to 14 and above).
Stage Seven: Loss of dinosaur name pronunciation skills and basic identification skills (teen years to young adult).
Stage Eight: Dinosaur Illiteracy (young adult and above). Apparently due to a lack of knowledge concerning the many new discoveries made and theories proposed since the adult was an expert at six or seven years of age.

I have also found that some people are dinosaur developmentally arrested at Stages Four, Five, or Six; and if you are participating in Dino Fest, you are probably one of them, as am I.

Most learning takes place in a developmentally sequential fashion that begins with simple information and/or skills and progresses to more complicated processes and functions. For example, people begin the process of learning to read by recognizing print as something "readable" and desiring to be able to read the print. They then begin to interpret print they see in the world around them, learning letters, phonetic sounds, and common words in the process. Soon they will read and comprehend phrases, sentences, and paragraphs using the basic skills they have developed. As time passes, a person's ability to read and comprehend more complicated printed materials increases due to the innumerable opportunities presented in life for practicing the skill of reading at many levels of difficulty. The average person does not pass through the stages of reading to the point of becoming a proficient reader, or an "expert," and then regress to illiteracy; nor would you find this serious regression in one's ability to write or to perform mathematical functions. So, why does it happen with the study of dinosaurs?

WHY STUDY DINOSAURS?

Several months after conducting a dinosaur workshop in Kansas, I was contacted by a teacher who had attended my training session. She was very upset. After the dinosaur seminar, she had gone back to her classroom excited about paleontology, and she had adapted her curriculum to include a thematic unit on the Mesozoic Era. Her students had thoroughly enjoyed the learning experience; however, before the unit was complete she attended another conference presented by one of the nation's leading proponents of thematic instruction. During the presentation the speaker commented on the importance of selecting broad thematic topics of relevance. According to the frustrated teacher, the instructor asked the following question of those in the audience, "Why would anyone want to spend instructional time and teacher energy studying something that has been dead for 65 million years, when there are so many current issues of global importance facing students today?" The Kansas teacher felt that she had made a mistake by incorporating prehistoric studies in her curriculum, and she asked me, "Why should my students study dinosaurs?"

The importance of studying dinosaurs is frequently debated. School superintendents and curriculum directors often feel that too much time is spent on high-interest topics that have marginal academic relevance, and the study of dinosaurs is often included in this grouping. When the study of dinosaurs is viewed in this light, it receives little attention when district curriculum guides are prepared. Regularly, textbook companies debate whether to include dinosaurs in their newest science series, and if they are to be included, at which grade level, since it is generally considered inappropriate to spend time teaching dinosaurs more than once or twice in a well-balanced K-12 science curriculum. Often, teachers who try to include an extra unit on dinosaurs are reproached by fellow teachers who inform them that dinosaurs are off-limits because they are a "second grade" theme, or whatever arbitrary grade level dinosaurs have been assigned within that school district. Parents seldom begrudge a short study of dinosaurs, but the worth of extended studies is often questioned. And since the study of dinosaurs evokes the question of evolutionary change as it relates to geological time, some parents are totally opposed to allocating any instructional time to dinosaurs. With this type of curriculum opposition, it is no wonder that the average student becomes less knowledgeable about dinosaurs with time.

TEACHER DIRECTED CURRICULUM

We must keep in mind that the vast majority of educational professionals involved in school administration, curriculum planning, and classroom instruction are functioning at Stage Eight of my growth and development chart. Dinosaur illiteracy is rampant among administrators and instructors in our schools, while the dinosaur experts are sitting at their student desks, waiting to be taught more highly complicated science principles based upon dinosaurs and the study of prehistoric time.

The fact that curriculums are usually controlled by Stage Eight adults influences the study of dinosaurs in many ways. Most importantly, the majority of teachers I have observed do not know enough about dinosaurs (paleontology) to make it a relevant part of their curriculum at any grade level. Frequently, dinosaurs are used as the focus of high-interest units that will be "fun" and a break in the "less fun" science curriculum. This type of attitude produces dinosaur units that have little academic importance; they become what I call "curriculum fillers." I can see why many administrators are ready to say, "Out with dinosaurs!"

Teachers who have not kept up with the most current discoveries and theories have difficulty teaching dinosaurs to students who have. It is embarrassing to hear six year olds correct the teacher's pronunciation of Pachycephalosaurus, or question outdated information presented by the teacher as "fact." I still hear teachers calling Pterodactyls and Mosasaurs dinosaurs, while informing students that giant dinosaurs had to live in water to help support their massive weight.

Dinosaurs will always be present in the commercial world, but it is even more important that they continue to be found in the academic world of our schools. The key to increased academic relevance is teacher education. Teachers need to be taken from Stage One (becoming aware of dinosaurs all over again) to Stage Four (becoming a dinosaur expert for curriculum enhancement) and this can only happen if they have closer contact with professional and amateur paleontologists. Schools need staff development conducted by dinosaur specialists. Teachers need to be constantly exposed to updated information on dinosaurs in curriculum-related newsletters and teacher magazines.

Paleontologists need to be actively involved in curriculum planning, K-12 in schools around the world. In a well-planned science curriculum, no student should ever progress from Stage Six to Stages Seven and Eight of my developmental charts. Even students who are more interested in English literature, European history, or computer sciences should always be interested "in viewing a dinosaur exhibit or finding out more about a new dinosaur discovery." Stage Six illustrates the attitude of an intelligent person who wants to make learning a lifetime project -- this is the goal of education as a whole.

STUDENT DIRECTED CURRICULUM

We can become better educators by looking at the curriculum through the eyes of our students. Dinosaurs are usually a child's first truly scientific topic of study. Frequently, this study begins independently of an adult. As the child becomes aware of dinosaurs, he/she begins to ask for books about dinosaurs. Dinosaur books often become a child's first experience with reference materials and "research." Book illustrations are studied, and the physical characteristics of dinosaurs are analyzed as children draw their own prehistoric reptiles. Children group or sort dinosaurs by their physical features, such as horns, long necks, and plates. As children imagine dinosaurs as once-living creatures, they begin to investigate their methods of movement and their dietary needs. Huge teeth in gigantic mouths on strong bodies that move quickly are

fascinating to children, especially because the dinosaurs are dead and present no threat when the lights are turned off at night.

Even a child with an average interest in dinosaurs can also be exposed to the following science principles by studying dinosaurs: reproduction and the development of young, predator and prey relationships, habitat importance, defense techniques, extinction (cause and effect), fossil formation and exposure, geological time, plate tectonics, mountain building, volcanoes, botany; and the list goes on indefinitely. Natural curiosity and the desire to know about dinosaurs plunges young children into advanced science studies enabling them to learn more about science as a whole while investaging a part -- dinosaurs and prehistoric time.

Students become more interested in learning content area subjects when these subjects are based upon the study of dinosaurs. With the guidance of an interested and informed adult, the study of dinosaurs can mushroom to include all subjects of a well-balanced curriculum: language arts, literature writing, social sciences, history, government, geography, and mathematics. When dinosaurs are the topic of study, students are interested in reading fiction and nonfiction, writing research papers and keeping journals, plotting discovery sites on a world map, graphing data, determining mass, etc.

CURRENT TRENDS IN EDUCATION

Several of the current trends in education use themes or topics to weave all academic subjects together to form a complete tapestry of interrelated knowledge instead of isolated threads of information. Paleontology should be woven throughout the tapestry of education, not isolated to a particular grade level and/or content subject -- science. If professional and amateur paleontologists are to become more involved in curriculum planning, staff development, and writing for teacher magazines and newsletters, they must be aware of current educational research and innovations.

Chief Seattle of the Duwamish tribe (1850's) said, "All things are connected." The typical school curriculum has not been organized with this thought in mind. Instead, if one formed a philosophy of learning based upon lesson plans, scheduling, and departmentalization, it would be, "All things are isolated." Even in self-contained elementary classrooms where students have one teacher for all subjects, the academic day is divided into time frames for studying the required subjects. In America, a nationwide restructuring movement has led many schools to consider implementing **interdisciplinary curriculums.**

There are several arguments for restructuring our K-12 curriculum in an interdisciplinary manner. In the early 1900's, the curriculum was very limited. Teachers taught English, science, history, geography, and mathematics at levels appropriate to a student's age and ability. Over the last fifty years there has been a tremendous knowledge explosion. Today, there is so much for a student to learn that it is nearly impossible to designate a class for each subject of importance. Many educators feel that with broad-based themes, subjects can be combined in a way that allows students to interrelate information in a more meaningful manner and that, in turn, students would be better prepared to apply what they have learned in one situation to another. For example, when teaching an interdisciplinary thematic unit on prehistoric time, information on the ratio of predators to prey might be included. Students would learn that fossil records indicate that there were many more plant-eaters in a region than meat-eaters, and why. The reasoning behind the "why" of this activity is relevant to any study of animals at any point in time, in any location or habitat around the world.

Interdisciplinary teaching is a very student-centered approach to instruction. Another modern trend in education is also very student-centered -- whole language. Whole language is based upon the idea that people "acquire language through actually using it for a purpose, not through practicing its separate parts until some later date when the parts are assembled and the totality is finally used" (Altwerger, Edelsky, and Flores (1987), p.145). When language is looked upon as a whole, the separate parts, such as letters, sounds, blends, and basic sight words are taught as the child interacts with real print, not contrived stories from a reader. Literature is used frequently, often to the exclusion of textbooks, and students are immersed in an environment of print. In a whole language classroom, it is important for the teacher to constantly demonstrate the importance of a life of learning. For example, the teacher demonstrates that reading is important by reading orally to students, by reading silently in front of students for relaxation and pleasure, and by using different types of reference materials frequently to obtain needed information.

Whole language classrooms often base their instruction on themes, and student directed projects are important to the learning process. Most whole language teachers also teach subjects besides language arts in a holistic manner, incorporating science, social studies, math, etc. into the thematic units in realistic ways. A teacher who is well educated in the sciences will know how to incorporate the

sciences into holistic thematic instruction and student
directed projects, thus constantly integrating earth science
and paleontology into the entire K-12 curriculum.

CONCLUSION

Interdisciplinary instruction and whole language are only
two of the modern trends in education that lend themselves
to the serious inclusion of paleontology in the K-12
curriculum. Others such as cooperative learning, thinking
skills programs, mastery learning, and outcome-based
education, also offer innumerable opportunities for the
integration of prehistoric life and geological time into the
overall curriculum; however, it is the responsibility of
those of us who know the benefits and importance of these
studies within a curriculum to speak with a united "voice"
as local, state, and national curriculum innovations are
planned and implemented.

After years of analyzing, debating, and discussing the
importance of teaching dinosaurs, and after hundreds of
visits to K-12 classrooms involved in the study of
dinosaurs, I (Zike 1994, 1993) have concluded that it is
important to include paleontology and its many branches of
study, at multi-grade levels within a well-balanced K-12
curriculum. It is not the destiny of the average adult to
become dinosaur illiterate; it is the design of the average
K-12 curriculum that causes this tragedy. The exciting news
is that the tide can be turned with curriculum reform, and
those who are "dinosaur developmentally delayed" must lead
the movement.

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How to Fight Dinosaur Abuse

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We are surrounded by dinosaurs. From toilet paper to teacups, television specials and Hollywood films, and more than 300 current books, dinosaurs are as ubiquitous as Ninja Turtles. But dinosaurs are no fad, as merchandisers have belatedly realized. They are a rite-of-passage for the young, a fascination that grips every generation.

Our love for dinosaurs is beyond reason. We loved dinosaurs when they were presented as elephantine behemoths, as cold-blooded sluggards. And we love them all the more now that explorations indicate some were as smart as ostriches, as swift as foxes (not as swift as cheetahs nor as smart as chimpanzees, except in the imaginations of Messrs. Crichton and Spielberg), as small as turkeys, as maternal as Donna Reed, as hot-blooded as Madonna, and that all endured far longer than we. World-dominant and immensely varied in form, habitat and behavior for 160,000,000 years, dinosaurs were, arguably, the greatest of all evolutionary success stories.

We often hurt the ones we love. The fact is dinosaurs are being abused. The dinosaurs don't object, but scientists and our children should, for also unlike the heroes on the half-shell, dinosaurs are the subject of a vibrant but gravely threatened science. And dinosaur abuse threatens our children's already woeful science education.

Dinosaur marketers have long failed to credit their scientific sources, or properly represent scientific findings. In all manner of commercial images from the wrongly tail-dragging Sinclair dino to the misnamed *'Brontosaurus'* (*Apatosaurus* is its right name) on Post Office stamps to catchy business book titles (Dealing with Dinosaurs), dinosaurs are still widely portrayed as dimbulb failures.

In our showplaces of science, our museums, what's presented on dinosaurs and dinosaur science is often dreadfully outdated or flat wrong. By its own former chief preparator's admission, the Smithsonian National Museum of Natural History, one of the best, displays a stegosaur with too many plates, an allosaur with a toe on the wrong side of its foot, and a horned dinosaur with a duckbill's foot. In many other natural history museum displays, no indication is given of which parts of any of the fossils are casts, which actual bone.

Worse than the inaccuracies is the inadequacy of the public information on dinosaurs. Staid and static exhibits further the mistaken notion of science as a set of facts, commandments found on high by the chosen few. Such exhibits communicate nothing of the process of paleontology, the disagreements and the excitement that process engenders, nor the many aspects of behavior, physiology or evolution it has addressed.

As a result of commercial misrepresentation and institutional neglect of a science, a child's dawning interest in science is often squashed permanently, a process paleontologist Stephen Jay Gould calls "the dinosaur rip-off."

And the rest of us remain caught in time-worn misperceptions of dinosaurs. Most Americans, according to a recent poll, believe dinosaurs lived at the same time as primitive humans, when we missed each other by 64 million years.

But the dinosaur myth most in need of debunking is the popular notion that the study of dinosaurs is a broad endeavor, deep in data. At present, when it comes to dinosaurs and dinosaur paleontologists, we haven't got many of either. Dinosaur science has made great strides of late -- half of all dinosaurs were found in the last two decades. But the world only knows 300 kinds of dinosaurs, and there are only 30 dinosaur scientists out looking, on a total world budget of less than $1,000,000.

Only a handful of American museums have a dinosaur scientist on staff or directly support dinosaur paleontology (while dinosaurs rank second only to physics as science museum exhibit themes). Within the United States, few universities, even those with vertebrate paleontology faculty, sponsor dinosaur excavations at home or abroad, nor enterprising symposia like DINO FEST. Those institutions that do dig dinosaurs are caught between a fossil-bearing rock and a hard place.

Case in point, Brigham Young University. In the summer of 1988, Kenneth Stadtman, a paleontologist at Brigham Young University, discovered a dinosaur pelvis eight feet around. The discovery came as his crew was about to break camp in Western Colorado after exhausting the university's less than $20,000 annual fieldwork budget.

Stadtman's find was promptly heralded in newspaper articles and television news programs around the world as the largest dinosaur bone ever found, from the largest of all dinosaurs.

Moreover, the discovery presented an anatomically significant and distinctive element of an animal and of a fauna -- giant browsing dinosaurs from the Late Jurassic Morrison Formation -- a long-mysterious community lately far better understood.

For his part, Stadtman believes larger dinosaur bones exist. They have already been excavated. Indeed, they may reside across the parking lot from his Provo, Utah laboratory. The basement of the BYU football stadium contains more than 50 tons of dinosaur bones, locked in huge plaster jackets. They were collected as long as two decades ago by Stadtman's mentor, 'Dinosaur Jim' Jensen, but the university has never raised the money needed to prepare the specimens. The recent discovery of *Utahraptor*, largest and earliest of the fierce deinonychid predators, in part in BYU's existing collection, demonstrates the hidden value of located but unplumbed paleontological treasures.

BYU has one of the nation's few and best-known dinosaur paleontological research programs. Yet it is so strapped for funds, even to maintain its collections,

that its single paid preparator was laid off temporarily and its curator has sold scraps of dinosaur bone in its gift shop.

More than an unfortunate irony, the disparity between funds generated by dinosaurs and funds allocated to those who study dinosaurs threatens the very future of the discipline.

Meager funding for all manner of scientific research is typical worldwide of many economically ailing nations. And in the United States lack of financial support is a common complaint of practitioners of many sciences.

But whether by the standards of the newer biological disciplines, where millions are awarded for gene manipulation studies, or by the far less exalted budgets of 'soft sciences,' paleontological research comes cheap. The total annual expenditure on dinosaur research in the United States and Canada combined is scarcely $600,000, by University of Pennsylvania dinosaur paleontologist Peter Dodson's recent estimate. And that paltry sum is quadruple the figure from a 1980 study by Canadian dinosaur paleontologist Dale Russell.

Elsewhere the profession's funding crisis is even more dire. In the Mongolian People's Republic and in Argentina, two of the four other nations richest in dinosaur faunas, dinosaur paleontologists have but a single balky vehicle for field research.

In a third of the dinosaur-rich countries, China, the national Institute for Vertebrate Paleontology and Paleoanthropology operates on an annual budget of $250,000. From that funding it seeks to maintain 120,000 (largely uncatalogued) fossils, and provide all living expenses for 160 resident scientists and 260 employees. In search of desperately needed foreign capital, Chinese officials exported so many of their remarkable dinosaur fossils -- to three international exhibitions -- that half the exhibit space of the Natural History Museum in Beijing was converted to a furniture showroom.

Within the United States few universities, even those with vertebrate paleontology faculty, sponsor dinosaur excavations at home or abroad. By the modest budgets of these university departments, dinosaur-digging and preparation is prohibitively expensive. Dinosaurs are commonly found in remote places. They require manpower and often heavy equipment to excavate.

Some institutions have solved their fossil funding crises radically, by disposing of their fossil collections entirely. So, Princeton University recently 'de-accessioned' its fossils to Yale and Yale may now be faced with the same dilemma.

The future of paleontology is imperilled by a manpower shortage as much as a financial one. There are less popular careers than studying dinosaurs, even within the small world of paleontology. But not many. There aren't, for example, enough fossil turtle experts in the world to field a softball team. As for dinosaur field researchers, their names couldn't fill a professional football team roster. During the 1992 field season there were fewer than 30 paleontologists out hunting dinosaurs.

Given that dinosaurs are often a child's introduction to science, and an awe-inspiring, captivating one at that, it's at least superficially surprising that more young people don't hew to that first calling. Indeed, a recent survey of vertebrate paleontologists by dinosaur paleontologist Wann Langston, Jr. indicated most had proceeded with careers following a youthful fascination with fossils.

The paucity of dinosaur researchers is ultimately linked to money. Of course, academia as a whole is not where the money is (the average salary for American university full professors was (as of my most recent figures, seven years old) $45,520, assistant professors just $27,920. Nor are vertebrate paleontologists attractive quantities to universities which realize, as required overhead, 40%, 60%, 75% or more of the grant funds their researchers win. Players for the big N.I.H., private medical foundation or corporate dollars make for far more desirable hires.

Women don't often enter vertebrate paleontology, for the same reason men don't, reasons Wellesley College paleontologist Emily Giffin: "money." Case in point, Jill Peterson, a particularly promising paleontological student. Peterson won the Society of Vertebrate Paleontology's Romer Prize for best student paper in the field when she was still an undergraduate at the University of Colorado. After graduation she dropped out of the profession in favor of marriage and now biology. "Paleontology just doesn't pay well enough to stick with it."

Certainly, there are tenured vertebrate paleontologists who make a comfortable living. But tenured positions are especially hard to come by in vertebrate paleontology, a hoary subject with no high-tech gloss and no corporate ties. The Society of Vertebrate Paleontologists numbers but 1,200 members. Only a small minority of those are students and amateur fossil collectors, yet scarcely only one-third of all SVP members are actually employed in the profession.

The dinosaur research totals -- 30 professionals searching for fossils, another 60 researching the subject, on less than $1,000,000 total budget on field research worldwide -- are embarassingly modest compared to the money made on dinosaurs. But are these resources insufficient? It can be argued that dinosaurs do not present a particularly rewarding realm of biological research. If a scientist seeks to address the fundamental nature of evolution, its pace and pattern, then clams, alligators, and any number of other groups of organisms would seem better candidates for study. All these creatures have lived longer than dinosaurs did, and there are more of their kind known, from today's world and the fossil one.

"New ideas are rare," Harvard University evolutionary biologist Stephen Jay Gould told me in the course of an impassioned if unconvincing peroration against dinosaurs (Gould was also converted to paleontology by a youthful fascination with dinosaurs). Paleontology is about the search for illustrations of evolutionary principles and, said Gould, "you can never get ideas applied to everything, but examples are more likely to emerge elsewhere than from dinosaurs."

On the whole Gould's point stands. But as neither he, nor other paleontologists knew at the time he pressed the argument to me, he could have used dinosaurs as an example of more than one evolutionary theory, as dinosaur studies have made several significant advances in areas of evolutionary research well worth further investigation.

Contemporary dinosaur paleontology has discerned much of dinosaur biology -how, and in what relationship to other dinosaurs and contemporary organisms, did dinosaurs grow, live, diversify, prosper.

In Mongolia, South America, India, and western North America new dinosaur finds upset accepted models of continental formation and movement. At the same time, these and other discoveries in Transylvania and Montana support evolutionary concepts of conservativism and diversification among species tracking changes in their habitats.

From China, India, North America and South America researchers have found abundant evidence of dinosaur social life, detailing much about behaviors only dimly glimpsed before, from Asian egg finds and North American footprint assemblages. A host of egg finds to follow Horner's of a decade ago, by him and others in Canada, China, Argentina, and India, show dinosaurs huge and small were egg-layers. Studies of embryos and young dinosaurs of many ages from Montana and western Canada provide the first detailed evidence of their growth patterns, and striking parallels to living organisms in the 'cuteness' of dinosaur babies, and the delayed acquisition of threatening characteristics among adolescents.

Juvenile dinosaurs, unknown a decade ago, now are catalogued in such number and age distribution that developmental changes in both duckbilled and horned species can be employed, as Gould did the evolving face of Mickey Mouse, to validate retarded development of many aggressive features. If these are not retained, neotenously, into adulthood, they do endure long enough in youth to inspire parental protection. Other new dinosaur findings illustrate strikingly the theories of how new species themselves are formed in geographically isolated populations, a concept developed by Gould's Harvard mentor, evolutionary biologist Ernst Mayr.

Experimental work is also greatly furthering current dinosaur research. Dr. James Farlow and fellow Indiana University/Purdue University researchers have performed sophisticated tests to gauge the mechanics of dinosaur stride and the processes of footprint fossil formation and weathering of fossils in channel deposits. Montana State University paleontologist John R. (Jack) Horner, in addition to many field discoveries of late, has established the first dinosaur histology laboratory to further his attempts to asses physiology, age, and genus of dinosaur by fossil bone characteristics. (Horner's research was funded first by his own McArthur Foundation 'genius' grant, then by his own and university fund-raising efforts facilitated by press attention to Horner's work).

Promising new techniques are being developed for CAT-scan analysis tied to injection-molded casting of portions of delicate and rare dinosaur fossils previously unavailable for study without irreparably damaging the fossil.

New technologies for locating fossils are being tested on dinosaur finds in New Mexico. By Utah State paleontologist David Gillette's enterprise, institutional grant or individual voluntarism, Los Alamos, Sandia, and Oak Ridge scientists have attempted to locate fossils by magnetic, infra-red, radar and acoustic testing with some good early results.

Paleochemical analyses of dinosaur fossils at Los Alamos (done on a volunteer basis at U.S. laboratories) are uncovering insights into the still dimly understood processes of fossilization. Scientists at University of Glasgow laboratories are isolating amino acid constituents of dinosaur tissue to the near-molecular level of determinants. Mary Schweitzer of Dr. Horner's lab at the Museum of the Rockies appears to have isolated dinosaur DNA from a red blood cell in a *T. rex* femur. Such studies may soon lead to microbiological identification of dinosaurs by family or even genus from a tiny fossil, and to a clarification of the evolutionary relationships among dinosaurs and between dinosaurs and their nearest avian and reptilian relations.

Dinosaur studies have leapt ahead lately, and the field continues to change, fast, as Gould is quick to point out. Whereas once the work was "highly descriptive with some speculation about adaptive values, done mostly by geologists who picked up some anatomy and had very little ecological knowledge," contemporary paleontologists are "far better trained in ecology, taphonomy, evolutionary theory."

Meanwhile, the business of much of the first century of dinosaur science, the naming of new dinosaurs, goes on, at an accelerating pace, notwithstanding the lack of funding for field work. Nearly half of all known dinosaurs have been named in the last twenty years. By Professor Dodson's own tally, more than 120 dinosaur genera have been recognized in that time, at a rate of seven new-named dinosaurs a year.

Little of the more sophisticated aspects of this ongoing dinosaur research has attracted public notice and support. Yet through an attention to dinosaurs in museum displays and publications unrivaled by any other fossil life, as DINO FEST testifies to, the public has acquired an understanding of, as well as affection for, dinosaurs. Yet that understanding is deeply flawed.

Outdated, one-sided and sensational popular books, staid and static exhibits, clunky toys and silly science kits, further mistaken views of dinosaurs, and, worse, the mistaken notion of science as a set of boring facts, commandments found on high by the chosen few. Such materials communicate nothing of the process of science, the disagreements and the excitement that process engenders, nor the many aspects of our own lives -- behavior, physiology or evolution, it has addressed.

How is that misunderstanding, and neglect of dinosaur science, and all of science for that matter, to be corrected?

Perhaps by scientists. Increasingly, scientists find themselves in roles for which they have little interest, and many, little talent -- fund-raising, political lobbying, commercial designing and media haranguing. For many years, researchers have devoted much of their working lives to soliciting grant support from increasingly inattentive and insolvent governments and corporations.

But of late, some researchers have taken their case directly to the public and the business community. Tropical biologists, faced with the disappearance of their entire data source, have been particularly successful in rallying public and governmental support. The time has come for many other sciences to do the

same, not only to save their disciplines, but to ameliorate the public's woeful lack of scientific information and interest.

Where is this money to come from? Not from overburdened and unwilling governments. At least indirectly, dinosaurs do contribute disproportionately to what public support exists for scientific research. As British paleontologist Michael Benton argued in New Scientist Magazine the public interest in dinosaur discoveries makes taxpayers more inclined to fund all of paleontology.

And what of universities themselves? The natural sciences departments of many universities now benefit directly from the appeal of dinosaurs. Dinosaur courses, now widely offered to American undergraduates, help sustain, by their popularity, the geology and Earth science departments of many universities. So concluded Bruce McFadden, a Florida Museum of Natural History paleontologist and past president of the Society of Vertebrate Paleontologists, in a May, 1989 Geotimes article entitled "Dinosaurs rescue geology departments."

Geology department enrollments have declined significantly in the past decade. To regain their audience, they have turned to dinosaurs, even though historically, as McFadden noted, "vertebrate paleontology has been considered by some an extraneous discipline in geology departments." McFadden surveyed 55 geology departments in American colleges in 1988 and found that nearly nine in ten of the 27 respondents had initiated survey courses designed to increase enrollment at their institutions, "with dinosaurs and geology of the national parks being the most popular...In most cases enrollments in dinosaur survey courses far exceed those in other newly insituted courses, sometimes by a factor of two or more... For large public universities, enrollments in dinosaur courses range from about 150 to 750 students."

McFadden himself taught a "Dinosaurs and Darwin" course for two years at the University of Florida, which though unadvertised and unlisted in course catalogs, drew a capacity crowd to a 150-seat lecture hall.

But, again, most universities are not sufficiently well-endowed to permit a substantial reordering of funding priorities, even for so obviously appealing a discipline.

There are a very few exceptions to the rule of taking dinosaur data without giving back to the data-collectors. Paleontologist Robert Bakker (an unpaid adjunct curator at the University of Colorado) gets a fee from the Tyco Toy Company for helping design the 'realistic' plastic dinosaurs on which the toymakers mount radar and ant-men with stun guns. Bakker and fellow dinosaur paleontologist Jack Horner collect honoraria for their advice to rival designers of those clicking motorized dinosaur replicas enormously popular in museums. These robot dinosaurs are disparaged as "prophylactosaurs" by paleontologists, but have proved immensely popular in science museums worldwide. Dinamation, the company Bakker advises, has established a philanthropic fund to finance fossil preparation of dinosaurs.

Dinosaur paleontologists themselves, Bakker and Horner aside, have little to show for the popularity of their work. The almost universal unwillingness of the most appropriate dinosaur research funding source, the commercial dinosaur-

exploiters from toy makers to science museums, to pay or even acknowledge their debt to paleontologists, is a disgrace.

Problem is, dinosaurs aren't trademarked. They don't earn royalties and ancillary rights from every tie-in that uses their name or their likeness. Their creator is apparently uninterested in remuneration. But next to nothing goes to the researchers who find fossils, name species, describe animals, interpret lifestyles; in short provide all the fossil fuel for the relentless engines of commerce to burn.

What can be done? A group of dinosaur scientists and popularizers, myself included, have banded together to fight, or rather work cooperatively with, commerce, for the rights of dinosaurs and those who study them.

The organization began with the nearly simultaneous boiling-over of many not normally volatile tempers. For Dr. David Weishampel, a dinosaur researcher at Johns Hopkins University, the last straw was an animated dinosaur film he watched with his children, and which like so many before it, made almost no reference to what is known about dinosaurs. For Dr. Peter Dodson, dinosaur researcher at the University of Pennsylvania, the call to arms came both from compiling figures on the paucity of worldwide research funding and encountering a run of awful popular books misrepresenting dinosaurs. For me, it was shame at accepting free meals and tent space from researchers whose entire summer's program operated on a budget smaller than that which a popular magazine had offered me for reporting on their work.

Our effort is but three years old but it has already begun to show fruitful results, chiefly through the sagacity of a former paleontologist turned businessman, Dr. Steven Gittelman and the generous support of exhibit developer Peter May. We have enlisted researchers, writers, artists and educators in the cause. We will award $500,000 in grants in the next 18 months and have raised more than $1 million.

We call ourselves, and our international non-profit organization The Dinosaur Society and we are working with manufacturers to create more accurate and up-to-date dinosaur products. We provide scientific specialists' advice (for a fee paid to scientists), on the preparation of new and more accurate books, toys, games and exhibits. We endorse noteworthy products and publications, lending our seal of approval as a badge of scientific acuracy which should result in increased consumer interest, and fees from manufacturers. We attempt to interest advertisers in featuring dinosaur research. And some scientists have offered to name their new-found genera and species for benefactors (a long-standing though little-recognized tradition).

To our pleasure, and frankly surprise, many manufactureres have expressed great interest in availing themselves of scientific services and supporting our research and educational mission, whether out of enlightened self-interest or genuine community concern.

On our own, we disseminate current and accurate information about the science to the media and directly to the public through press releases and to our individual subscribers via a quarterly news bulletin or a monthly children's

newspaper with many thousand scubsribers, DINO TIMES. We offer speaking programs and tours to the public led by scientists. And we have begun working with museum and exhibit designers to make more engaging and representative displays of the science and the dinosaurs themselves, such as our Dinosaurs of Jurassic Park exhibit which has toured natural history museums in New York, Boston and Ft. Worth.

To spend our revenue we set up our own committee of scientific reviewers, and they devised an application, so that grants of modest size could be distributed worldwide as funds become available. Proceeds from this non-profit endeavor will go to funding a host of research and educational projects in dinosaur science.

This effort has resulted in significant, enduring support for dinosaur paleontology and other related sciences and arts. Whether its model can be applied to other scientific disciplines with less of a hold on public attention remains to be seen.

We can only hope more science-profiteers will begin to acknowledge their debt to science and scientists. If not, dinosaur paleontology, and many other sciences, are headed the way of the dinosaur, or the dinosaurs as we once perceived them, outmoded failures.

It is to be hoped by all who work on and fantasize about dinosaurs that dinosaur science will neither starve in poverty nor drown in commercial silliness. Instead, it may yet take glorious flight, like so many of today's dinosaur descendants, the birds.

--Don Lessem is founder of the Dinosaur Society, host and writer of NOVA documentaries, author of Dinosaurs Rediscovered and several other dinosaur books for adults and children. He is children's dinosaur editor of Highlights Magazine. For information on the Dinosaur Society's programs and publications write The Dinosaur Society, 200 Carleton Avenue, East Islip, NY 11730.

Deinonychus, The Ultimate Killing Machine

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Speculation about the behavior and life activities of any kind of extinct animal seems to be a waste of time. But people are curious, and they do it all the time. Their favorite subjects, of course are dinosaurs. You don't have to be an expert and it doesn't cost any money. Anybody can do it. Did *Diplodocus* swim? Or just soak in those Mesozoic lakes and streams? Did *Tyrannosaurus* chase its prey, or did it just scavenge on left-overs? Did *Mononykus* burrow in the ground to hide its head, or did it just scratch its arm pits? It is obvious that it didn't fly, but it must have run fast. You don't have to be a paleontologist, or an ethologist. In fact, it is probably an advantage not to be a scientist at all. (How come? Then you're free to let your imagination run wild. That sure would help *Mononykus* .) The only equipment you need is a powerful imagination, some common sense, and a certain amount of evidence. That evidence will be the clues, the tips that stimulate your imagination--in this case, how a long-dead animal that lived many millions of years ago behaved. Let me show you how that works.

The animal I have chosen for this demonstration is the Early Cretaceous dinosaur *Deinonychus*. That is the name that I gave to a new kind of dinosaur that I discovered back in 1964, after a number of years of exploration. If you saw the movie "Jurassic Park", you saw the animal I have in mind. There it was called *Velociraptor*, but in reality it was *Deinonychus*. As you know from the film, *Deinonychus* was a very unusual kind of animal, one that had never been seen or imagined before. The challenge before us is to try to figure out how this strange animal lived, and what it could or could not do.
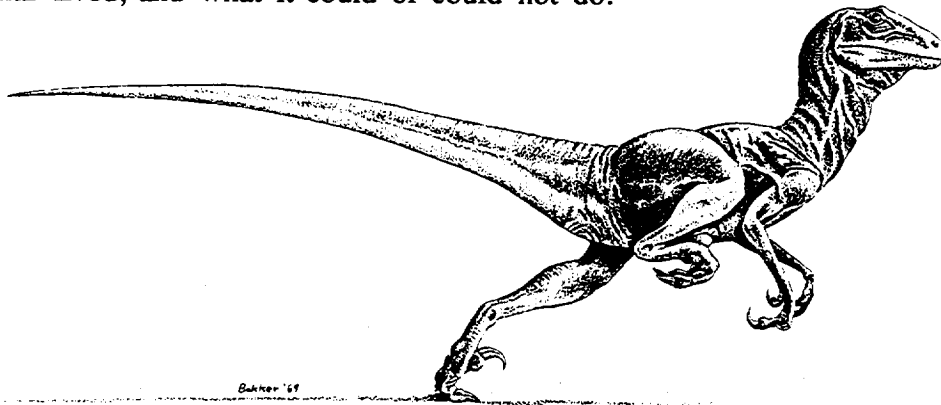
Figure 1. Artist's rendition of *Deinonychus* in life. (by R.T. Bakker)

Deinonychus (Fig. 1) was a medium- to small-size, two-legged, flesh-eating dinosaur of the kind that we classify as a Theropod Saurischian. It belonged to the same group of animals as *Tyrannosaurus*, *Tarbosaurus* of Asia, *Allosaurus* and *Coelophysis* of North America and many other kinds, all of which were carnivorous. We know that because all of these creatures had one very special feature in common; they all had sharp-edged, blade-like teeth. These teeth obviously were for cutting, tearing or slicing. Theropod dinosaurs also were *all* bipeds. That means that they walked or ran only on their hind legs. They all were required to move that way, or what is termed obligate bipedality. They could not possibly have stood or moved on four feet. You might not think that is too special because, after all, people do that all the time. And so do birds! (But people don't do what these other bipeds can or could do. There also may be a

Figure 2. Hand anatomy of *Deinonychus*.

very good reason why both birds and theropod dinosaurs are/were obligate or forced bipeds. It is very possible that today's birds are actually the living descendants of some theropod dinosaur.) We know that this manner of movement was true for *Deinonychus* because the forelimbs (arms and hands) were designed for grasping and holding objects (Fig. 2)--not for walking. Their hands were just not built for that. The most convincing clue is that the fingers (three in *Deinonychus*) of each hand ended in large curved and sharp claws or talons--talons very much like those on the feet of birds of prey, like the eagle, the osprey, and falcons and owls.

Another very surprising feature of these forelimbs in *Deinonychus* is in the shapes and arrangement of the wrist bones (Fig. 2). Unlike any other dinosaur known in 1964 when I found *Deinonychus*, the wrist design allowed great flexibility of the hands. These long three-fingered hands and claws could be turned toward each other (pronate and supinate), like human hands. This means that *Deinonychus* could actually hold objects--such as its next victim, the prey animal. The distinctive teeth of *Deinonychus* were sharp pointed blades with differently serrated front and back edges designed for slicing or cutting flesh, like a good steak knife, unmistakable clues that this animal fed on other animals. But what kinds of prey did *Deinonychus* seize in those jaws or grasp in its clawed hands? Other anatomical clues provide hints.

Several years before I stumbled across *Deinonychus* at the now famous Yale discovery site in Montana, my team of explorers found another partial skeleton of a different kind of animal. When it was exposed in the field, I realized that it was a member of the plant eating ornithischian dinosaur variety that we call ornithopods. (A bad name, because their feet were not like those of birds, which is what that term means.) Actually, I thought it was a particular kind of ornithopod termed *Camptosaurus*, and only later in our explorations did I realize that this specimen (and many others we found in those same strata) was a new kind, that I named *Tenontosaurus*, which means "tendon lizard". *Camptosaurus* was a well-known ornithopod, known from the Morrison Formation, but we collected it anyway and prepared it for shipment back to the labs at Peabody Museum at Yale. During the excavation, we discovered that the mid-section of the animal was missing, just as though a huge bite had been taken from it. Later that year when we prepared this specimen back at the lab, we found a single carnivore tooth (which explained the missing "bite") but, only later after discovery of *Deinonychus*, did I recognize this tooth was exactly like those of *Deinonychus*. That mutilated plant eater skeleton turned out to be a common variety in those Early Cretaceous rocks, and appears to have been a favorite food of *Deinonychus*, but more about that later. Unknown to me at the time, that was my introduction to *Tenontosaurus* - the "tendon lizard", a delicacy to *Deinonychus*.

So, our picture of the killer is taking shape: a small to medium size, 150 to 175 pound two-legged, hungry, predaceous dinosaur with long arms and clawed grasping hands and a mouth full of razor-sharp teeth. But, I haven't told you about the most important clue of all, the evidence that tells how *Deinonychus* killed its prey and why I created the name *Deinonychus*. That name means "terrible claw" and is in reference to one of the animal's most unusual and distinctive features--two very large and strongly curved sickle-like talons, one on each foot (Fig. 3)! These curved claws were very thin and undoubtedly sheathed by razor-sharp talons for the purpose of slicing open victims and disemboweling them with powerful backward kicks. *Notice*. These slicing blades were on the FEET of the animal that was an *obligatory* biped!

Figure 3. Foot anatomy of *Deinonychus*.

Now imagine: this must have been a highly active and agile animal that must have leaped repeatedly at its victims with slashing kicks. Even more interesting is the special anatomy of those killing sickle-bearing toes. In contrast to the other two normal walking toes of each foot (here the joints cannot be extended or bent back, but only folded or clenched = flexed), the killing talon-bearing toe could be bent back or hyperextended, as well as flexed. The special design of the killing toe allowed the big sickle claw to be carried well up in the air when walking or running so that the talon was kept from abrasion or damage against the ground. On the attack, *Deinonychus* launched itself at the prey animal with outstretched grasping hands and powerful backward slashes of its lethal feet.

That image is reinforced by yet another anatomical clue that was new and quite unexpected in any dinosaur. The novel clue is the highly specialized tail vertebrae stiffened by dozens of long rods of bone (Fig. 4). These appear to be ossified tendons that extended nearly the whole length of the tail, making it almost ram-rod straight and virtually inflexible. The tail apparently could be bent only at its base close to the hind legs. The bony rods actually are extensions of standard vertebral processes (anteriorly the prezygapophyses along the tops of the caudal vertebrae) and elongations of the haemal arches (beneath the tail). This strange tail anatomy had never been seen before in any animal, and is now known only in the related dinosaur *Velociraptor*.

Aware of those killing talons on the feet of *Deinonychus*, I soon realized that the tail provided a logical and essential piece of evidence that explained the activity and behavior of this very unusual animal. This caudal apparatus was used as a balancing beam, exactly like a tightrope walker's balancing pole, aiding *Deinonychus* in keeping its balance and orientation while attacking. (Think how a rigid pole is used by the high-wire circus acrobats to maintain their balance.) That is the reason why I chose the specific name *"antirrhopus"*, which means "balancing", in reference to the unusual anatomy and function of the tail of *Deinonychus antirrhopus*.

That caudal clue suggests something even more dramatic about the killing skills and behavior of *Deinonychus*--dare I say "acrobatic" ability? That balancing tail suggests that *Deinonychus* was a very active and extremely agile, acrobatic predator (Fig. 5), unlike any other. *Deinonychus* very probably attacked with both feet at once, leaping at its prey with both feet and both hands reaching forward for its victim. The painting by artist John Guerche of the Smithsonian Museum has vividly captured such a *Deinonychus* assault on a very much larger *Tenontosaurus*--leaping through the air with both deadly talons aimed at the victim's flank.

Figure 4. Tail anatomy of *Deinonychus*.

Figure 5. *Deinonychus* as displayed in an attack mode.

The final and best clue about *Deinonychus* attack behavior was most unexpected, and is the most important of all. As we probed, explored and excavated at the Yale *Deinonychus* quarry site (Fig. 6) during the 1965, '66, and '67 field seasons, we were puzzled by what we were finding. The quarry seemed to contain only carnivorous dinosaur remains--disarticulated skeletal parts (Fig. 7). Moreover, these fragments seemed to belong to just one kind of predator, although we could not be sure at the time. All told, at the end of three full field seasons, we had uncovered at least three, and possibly four or more different individual predators--all of them in pieces! There were three separate *Deinonychus* caudal series, several isolated single caudals, many foot and hand bones, skull elements and scattered teeth. These represented no less than three individuals, perhaps more. To our surprise, none of these were abraded or worn, as would have been the case if they had been transported and deposited by a stream, but rather they seemed to have been scattered at random over a relatively small area of perhaps 25 to 30 square meters, as if by a scavenging animal. Yet none of the fragments had tooth marks. We wondered why there were only *Deinonychus* remains. What killed all these individuals?
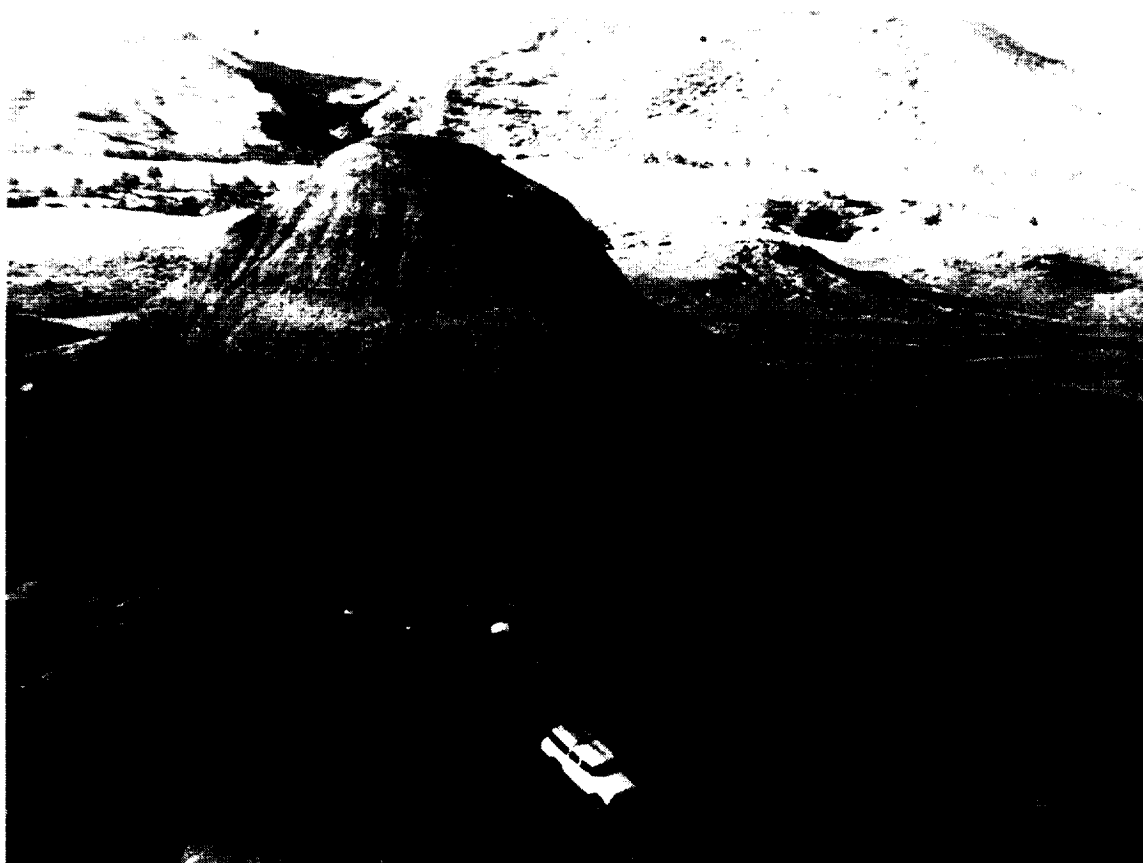
Figure 6. The Yale *Deinonychus* discovery site and quarry.

Yale Deinonychus Quarry (YPM 64-75)

Montana
1964 - 1967
John H. Ostrom

- Deinonychus bones
- Tenontosaurus bones
- Deinonychus teeth
- Tenontosaurus tooth
- Deinonychus cranial fragments
- ? A   Solitary Deinonychus caudal
- Scale (approx.)
  0 cm 9

N.

YPM 5202

? C

? A

YPM 5201

YPM 5466

YPM 5203

? B
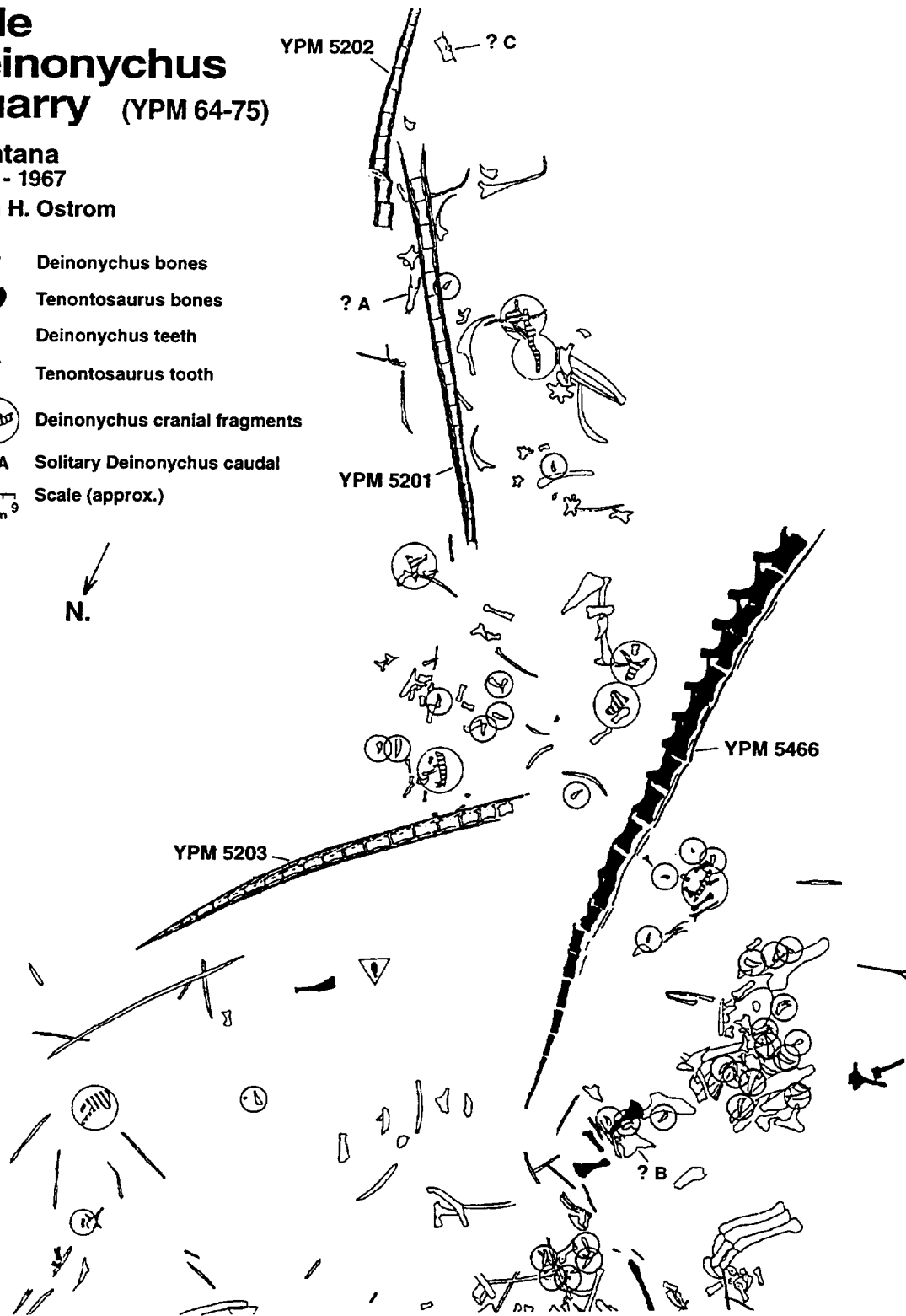
Figure 7. *Deinonychus* quarry map.

Then we made the most important and exciting discovery--another articulated series of caudal vertebrae. But this tail was different, and we soon realized that it belonged to *Tenontosaurus*! Here was the tail of the intended victim, the plant-eating *Tenontosaurus*. The multiple dead *Deinonychus* would seem to be the remnants of a band of predators and *Tenontosaurus* had been their objective. Here was the most significant evidence of all at this remarkable site. Here was virtual proof that at least some theropod dinosaurs hunted in packs, and *Deinonychus* clearly was such a predator. As far as I know, this is the first evidence ever found indicating that kind of behavior in any kind of theropod. It is not a surprising behavior in a predator, but it had never before been documented for any dinosaur.

Here is powerful (but not conclusive) evidence that *Deinonychus* must have been a pack-hunting animal. The evidence also indicates why. At least in this case, *Deinonychus* chose to attack an animal much larger than itself! (There is strength in numbers!) Actually, there were more predators than those we found because some survived to finish off the victim, and subsequent collecting at the site by the Museum of the Rockies teams have recovered parts of individuals that the Yale teams failed to reach. This mass attack takes on additional significance in light of nearby discoveries. Repeated finds at other sites show that *Deinonychus* apparently had a special preference for lunches or dinners of *Tenontosaurus* meat. Nearly every specimen of *Tenontosaurus* that we found was associated with isolated shed teeth of *Deinonychus*. In many cases, this was an exclusive association--only *Deinonychus* teeth were found in association! (It's almost as if no other predator was "allowed" to feed on *Tenontosaurus*.) The evidence seems clear that *Tenontosaurus* was the favorite food of this unusual killer, or at least was the most susceptible to *Deinonychus* assaults.

How many killers were involved in the kill at the Yale site is not known, but there were several more than the three or four that we recovered. Some others survived to complete the slaughter of the *Tenontosaurus*. Actually, there might have been many more than the *Deinonychus* casualties found so far. Thus, those fragmentary finds are evidence of only the minimum number of predators that were mortally injured by the intended prey animal in its struggles for survival.

No longer can there be any question about the pack-hunting strategy of this ultimate killing machine--*Deinonychus*.

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Tyrannosaurus sex

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ABSTRACT

The discovery in recent years of several well preserved and partially articulated skeletons of *Tyrannosaurus rex* has provided the impetus for a study of sexual dimorphism in dinosaurs. The fifteen significant specimens of *Tyrannosaurus rex* discovered to date may be divided into "robust" and "gracile" morphotypes. Examinations of extant crocodiles and birds show a link between musculature of sexual organs and sexual dimorphism of osteoskeletons. Analogous differences in articulated dinosaur remains point to a method of determining the gender of individual dinosaur skeletons and the presence of an intromittent organ in at least some species. For theropods, and particularly for *Tyrannosaurus rex*, the larger and more robust individuals are almost certainly female.

INTRODUCTION

"After eating, the most widespread habits among modern animals are those concerned with sex, and there is no reason to suppose that this did not raise its allegedly ugly head millions of years before Freud. Clearly if we are to regard our fossils as once-living creatures, consideration of sex must arise .." (Ager - 1963)

On August 12, 1990, while exploring the badlands of the Hell Creek Formation in North Central South Dakota, Black Hills Institute collector Susan Hendrickson came upon the remains of a large skeleton eroding from a Maestrichtian age (65 million years old) stream bed. As the specimen was excavated from the sediments at the base of the cliff where it was found, it became clear that this was no ordinary fossil. It was, in fact, the beautifully preserved skeleton of the largest and most complete *Tyrannosaurus rex* (Fig. 1, Tables 1, 2, 3) found to date. The skeleton was nicknamed SUE™ in honor of its discoverer. The subsequent collection and (incomplete) preparation of this marvelous fossil has yielded some surprising information about the functional anatomy of this best known but little understood dinosaur.

As the scientist "first on the scene" and most closely involved with the exploration of these uncharted waters, I have been privileged to the secrets of SUE™ as her bones whispered them into my ear. These whispers were sometimes very soft, as when I was faced with interpreting the significance of the presence of a broken and healed leg on this
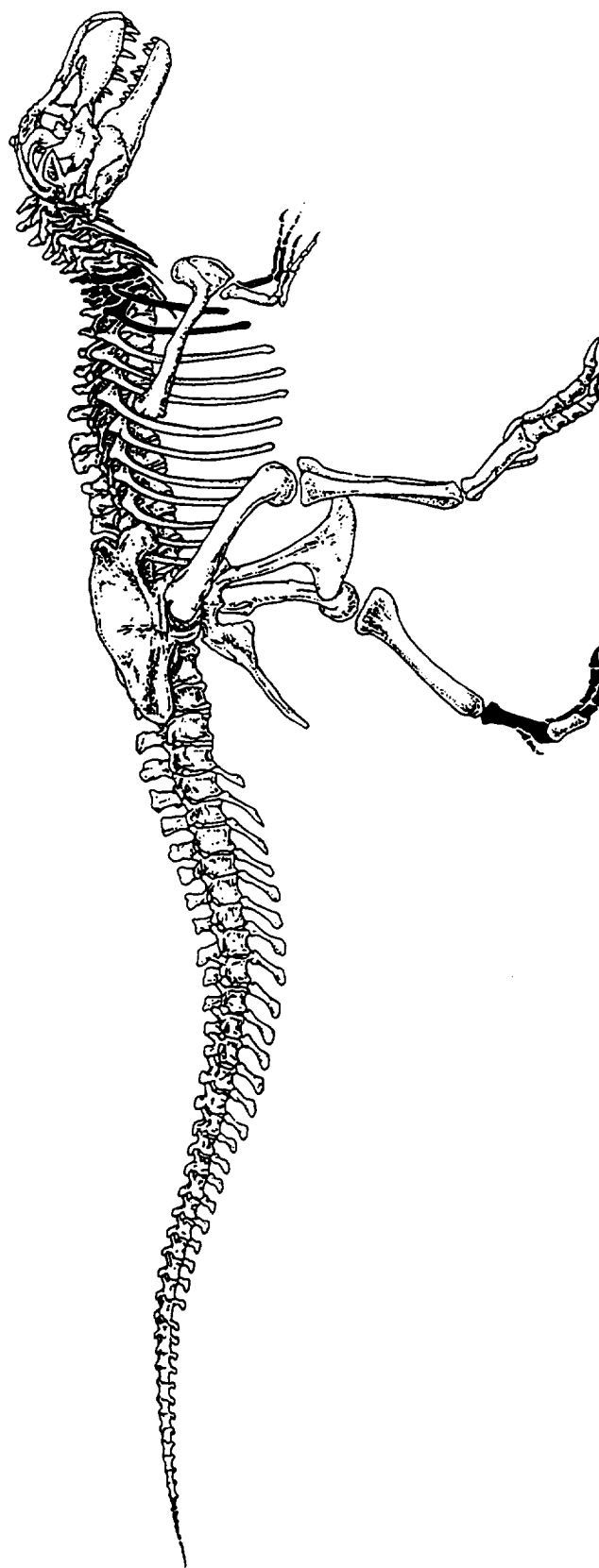
Figure 1

SUE™ *Tyrannosaurus rex*
Robust (female) Morphotype
Skeletal restoration - bones in black not yet seen
Total Skeletal length = 12500 m.m.   Skull length = 1530 m.m.

Illustration: Dorothy Sigler Norton

Table One

SPECIMEN CATALOG FOR TYRANNOSAURUS REX

ITEM NUMBER	SPECIMEN NUMBER	DISCOVERER *	YEAR	LOCALITY	SKELETON	ON DISPLAY	SEX **	MUSEUM & LOCATION
1	BM-R7994	Brown - P	1900	WY	25%	No	?	British Museum, London
2	CM-9380	Brown - P	1902	MT	40%	Yes	F	Carnegie Museum, Pittsburgh, PA
3	AMNH-5027	Brown - P	1906	MT	60%	No	M?	American Museum of Natural History, New York, NY
4	LACM-28344	Garbani - A	1966	MT	25%	Yes	M	Los Angeles County Museum, Los Angeles, CA
5	LACM-28345	Garbani - A	1966	MT	25%	No	?	Los Angeles County Museum, Los Angeles, CA
6	SDSM-12047	Floden - A	1980	SD	25%	Yes	M?	SDSM&T, Museum Of Geology, Rapid City, SD
7	TMP.81.12.1	Sternberg - C	1946	Alberta	25%	Yes	M	Royal Tyrrell Museum, Drumheller, Alberta
8	TMP.81.6.1	Student - A	1981	Alberta	70%	Yes	F	Royal Tyrrell Museum, Drumheller, Alberta
9	MOR-009	Hager - P	1981	MT	25%	No	?	Museum of the Rockies, Bozeman, MT
10	MOR-555	Wankel - A	1988	MT	80%*	No	M	Museum of the Rockies, Bozeman, MT
11	SUE, BHI-2033	Hendrickson - A	1990	SD	90%*	No	F	Black Hills Museum of Natural History, Hill City, SD
12	STAN, BHI-3033	Sacrison - A	1992	SD	60%*	Yes	M	Black Hills Museum of Natural History, Hill City, SD
13	MOR-008	? - ?	?	MT?	40% of skull	No	F	Museum of the Rockies, Bozeman, MT
14	Bowman	Pearson - A	1993	ND	?		?	Bowman, ND
15	DUFFY	Sacrison - A	1993	SD	20% to date		M?	Black Hills Museum of Natural History, Hill City, SD

Compiled by: David A. Burnham and Peter L. Larson: Black Hills Institute of Geological Research, Inc.

* C = Professional collector, P = Degreed paleontologist and A = Amateur paleontologist

** Note: There are two skeletal morphotypes: a robust form we believe is female and a gracile form we believe is male.

TABLE TWO

COMPARATIVE DATA
VARIOUS *Tyrannosaurus* SKELETONS

SPECIMEN ELEMENT ↓	BHI 2033	MOR 555	AMNH 5027 LENGTH ↓	CM 9380*	TMP 81.6.1
Skull length	1530	?	**1240	INC	1130
Skull width	960	?	860	INC	C
Femur	1380	1300	NONE	1300	1200
Tibia	1200	1090	NONE	1140	
Ilium	1525	1480	1515?	1515	
Metatarsal II	660	600		614	555
Metatarsal IV	630			600	
Humerus	391	382	NONE	368	292
Ulna	271	200			
Radius	175	165			

*Originally AMNH-973

**Straight line measurement down the midline of the skull from the back of the quadrates to the front of the premaxilla. Osborn's 1355 mm skull was a "wraparound" measurement.

TABLE THREE
SUE™ - BHI 2033

HIND LIMB

ELEMENT	LENGTH (mm)
Ilium	1525
Ischium	1270
Femur	1380
Tibia	1200
Fibula	1047
Metatarsal II	630
Metatarsal IV	660

FORELIMB

ELEMENT	LENGTH (mm)
Scapula-Coracoid	1385
Humerus	391
Ulna	271
Radius	175
Metacarpal I	67
Metacarpal II	113
II Phalange 1	55
II Phalange 2	81

VERTEBRAL COLUMN

ELEMENT	LENGTH-HEIGHT(mm)
Sacrum	980
First Caudal	200 - 640
Last Dorsal	145 - 780

First 37 Caudal Vertebra = 6350

(Probable Caudal Count = 46)

Total skeletal length = 12,500 mm = 41 feet, plus or minus 1 foot

SKULL

LENGTH (mm)	1530
WIDTH (mm)	960

Tyrannosaurus rex - Robust Morphotype
View of Right Side of SUE™'s Skull - Total Length = 1530 mm

Illustration: Dorothy Sigler Norton

Figure 2

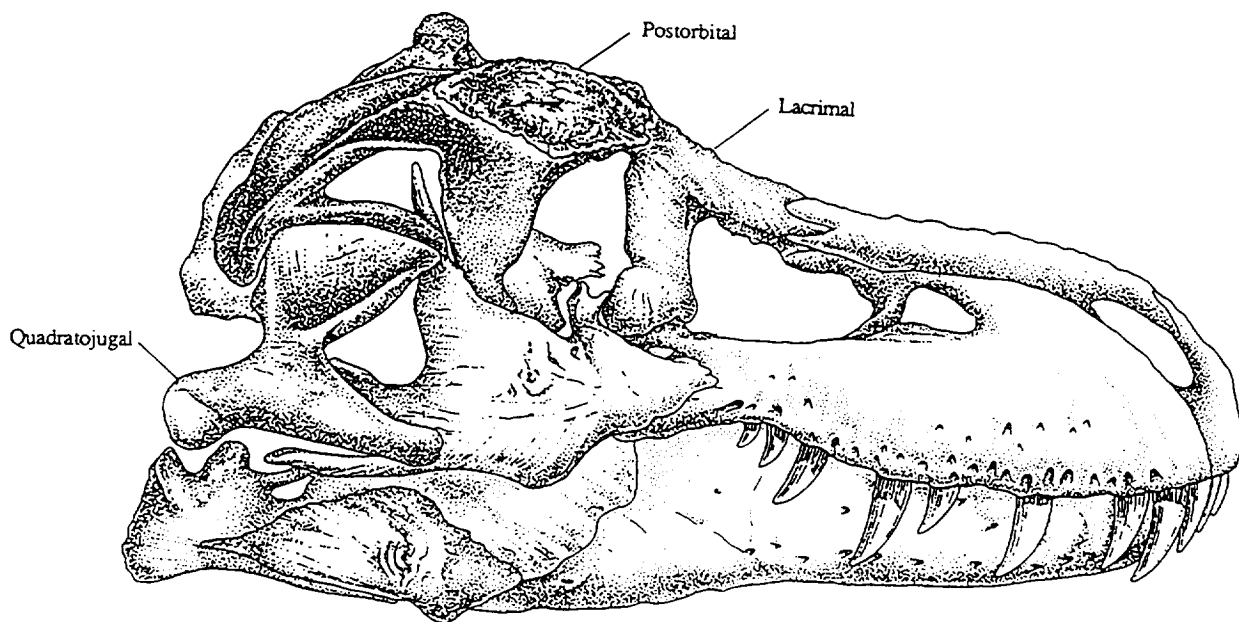fossil (how could a bipedal animal survive with one incapacitated leg?). However, there were times when these whispers were very loud, as when interpreting the closure of the mouth (Fig. 2). We found that the mode of operation of the jaws was as a "shear" rather than a "nutcracker", as had been envisioned. The teeth do not occlude but rather pass by each other as the lower jaws close and fit inside the upper jaws.

Probably the most interesting research we have been able to explore to date is that of sexual dimorphism. Even before SUE™ was completely excavated, her name brought up the question of gender. SUE™'s discovery started this investigation which has led to a probable means of showing sexually related skeletal differences in dinosaurs. The identification of the sex of a dinosaur skeleton is important to the science of paleontology because:

1. The recognition of sexual differences will help to unravel the classification of dinosaurs which currently may separate male and female into different species.

2. Knowing the sex of individuals will help us to better understand dinosaur behavior and social interaction as well as the function of certain portions of dinosaur anatomy.

PREVIOUS WORK

More than thirty researchers have explored the field of sexual dimorphism in dinosaurs. One of the earliest was O. Abel who, in 1924, proposed that perhaps some of the differences in cranial crests of lambeosaurines (a group of duckbilled dinosaurs), could be accounted for by the sex of the individual. Duckbilled dinosaurs have been the subject of nearly half of the published works on sexual dimorphism in dinosaurs. Ceratopsians (horned dinosaurs) have also attracted the interest of paleontologists and are the next most popular group in literature discussing sexual differentiation. More "robust" individuals with larger horns were thought to be males. It seems that most paleontologists who recognize sexual dimorphism, automatically and without supporting data, assign the larger, more "robust", or "hornier" individuals to the male gender.

The work of Raath (1990) and Carpenter (1990) who study carnivorous dinosaurs called theropods, in contrast, found the first evidence which challenged this male-mammal-chauvinistic view. Michael Raath looked at a bonebed of *Syntarsus*, a small Jurassic theropod. Studying the disarticulated remains of juveniles and adults, he found that as these dinosaurs reached maturity, their skeletons developed into two forms, or "morphotypes": a heavily built, or "robust", morphotype, and a lightly built, or "gracile", morphotype. Because these differences can be seen only in mature individuals, this strongly suggests that these are sexual morphotypes. Raath states: "The Chitake

Syntarsus concentration seems to be a case in point. If the morphological variation is indeed sexual, which morph represents which sex? It is intuitively tempting to regard the larger and more muscular forms as males, because of the widespread tendency among vertebrates for males to be larger and generally more muscular than females. But there are many exceptions to this generalization and merely to declare the robust individuals to be males would be facile and meaningless."

In the adults, he found that the robust individuals outnumbered the gracile and concluded that they must be female. Raath reasoned that there is an advantage to having a larger number of females in any given population. He also considered the possibility that the sexes might be geographically separated at certain times. Since the sample contained a significant number of juveniles it was logical to assume that females would be more reluctant to leave their young if a dangerous situation presented itself. To add to Raath's argument, it is, after all, the female who has the larger investment in the young and would therefore be most interested in their salvation.

Ken Carpenter, who studies large theropods including *Tyrannosaurus rex*, was one of the first to propose the existence of sexual morphotypes in this species. Carpenter, looking at the North American *Tyrannosaurus rex* and *Tyrannosaurus (Tarbosaurus) baatar* from Mongolia, defined differences based upon the humerus (arm - Fig. 3) and ischium (pelvic bone - Fig. 4) as well as the more general robust and gracile appearances of other skeletal elements. Carpenter, like Raath, concluded that the robust morphotype was female. This conclusion was based, in part, upon the shape of the ischium in the robust form, which allows for a wider passage for the laying of eggs.

Finally, Ralph Molnar mentioned a possibility of sexual dimorphism in *Tyrannosaurus rex* in his 1991 paper on cranial osteology. He suggested that the presence or absence of a rugosity on the postorbital (bone above and behind the eye - Fig. 2 & 5) could be a sexual difference. Molnar, however, did not comment on which sex possessed this horn-like knob of bone. As voluminous as the work has been, until the discovery of SUE™ , no one had identified a single anatomical character which would allow us to assign a definite sex to an individual skeleton.

TYRANNOSAURUS: SKELETAL DIFFERENCES

In gathering data for this study, along with searching the literature, I visited institutions in North America which house collections from Maestrichtian Age (68-65 million years ago) sediments. My intention was to locate specimens of *Tyrannosaurus rex* to see if
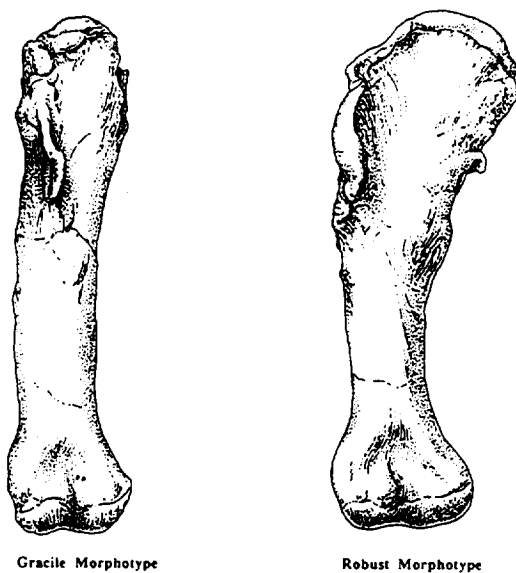
Gracile Morphotype   Robust Morphotype

Tyrannosaurus rex - Right Humerus
Anterior View

Illustration: Dorothy Sigler Norton

Figure 3

C

B

A
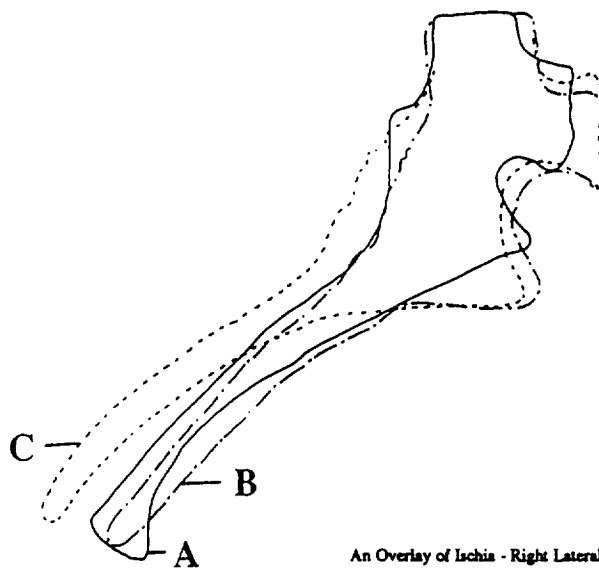
An Overlay of Ischia - Right Lateral View
A. CM9380; B. TMP81.6.1 = Female Morphotype; C. AMNH5027

Illustration: Ken Carpenter

Figure 4
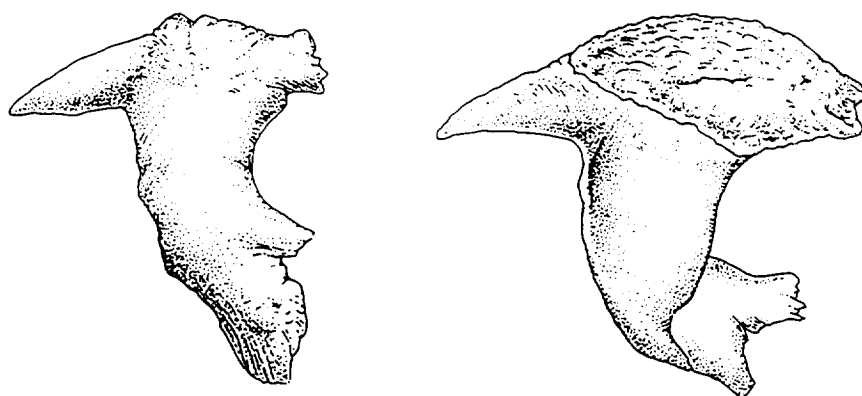
Figure 5

Gracile Morphotype   Robust Morphotype

Tyrannosaurus rex - Right Postorbital

Illustration: Dorothy Sigler Norton
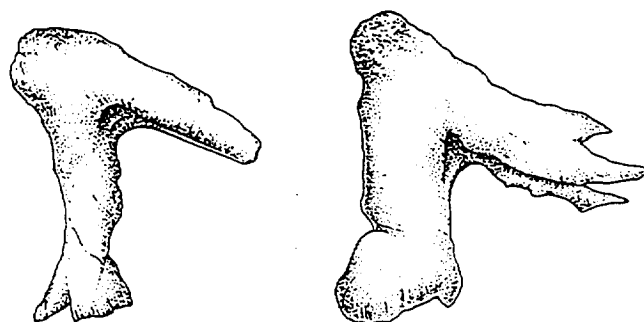
Gracile Morphotype   **Figure 6**   Robust Morphotype

Tyrannosaurus rex - Right Lacrimal - Lateral View

Illustration: Dorothy Sigler Norton

Gracile Morphotype   **Figure 7**   Robust Morphotype

Tyrannosaurus rex - Right Quadratojugal - Lateral View

Illustration: Dorothy Sigler Norton

differences could be identified, quantified and grouped. Some of the results of this survey may be seen in Tables 1 & 2. The fifteen specimens attributed to *Tyrannosaurus rex* may be divided into two groups, or morphotypes: a heavily built, or "robust" morphotype, and a lightly built, or "gracile" morphotype.

Upon dividing these fifteen specimens into groups based upon general "robust" and "gracile" characters, I observed that certain bones have recognizable differences which also fall within these two distinct groups. In the skull (Fig. 2), these bones include the postorbital (Fig. 5, the lacrimal (Fig. 6) and quadratojugal (Fig. 7). The humerus (Fig. 3), ischium (Fig. 4) and sacrum (Fig. 8) of the "robust" and "gracile" skeletons also show noticeable morphological differences.

It seems reasonable to assume that these differences are based upon sex rather than the existence of two distinct species of extremely large carnivores living contemporaneously in the same region. If these are indeed sexual differences, a mammalogist may be tempted to assign the larger, "robust" morphotype to the male gender. However, it seems more likely that the wider sacrum and more steeply angled ischium (both pelvic bones) of the "robust" morphotype would provide more room for the passage of eggs. Although this conclusion seems logical, it still does not make a clear case for anatomical differentiation based upon sex alone.

MODERN ANALOGY

Because non-avian dinosaurs have been extinct since the close of the Mesozoic Era, approximately 65 million years ago, it is impossible to determine the sex of individuals by the examination of soft tissues. Reproductive organs, unfortunately, are not preserved in any known specimen. Thus, we are left with the examination of extant forms which bear close relationship to these animals whose soft parts have long since decayed. Crocodiles and predatory birds seem to be the best candidates if we wish to reconstruct the reproductive mechanisms of *Tyrannosaurus rex* and perhaps find some skeletal basis for the sexing of dinosaurs in general.

BIRDS OF PREY

Paleontologists are not the only natural scientists to be plagued with male-mammal-chauvinism. Other biologists are human, too. Ornithologists have always cast a suspicious eye towards birds of prey. Why is it, they ask, that female raptors are
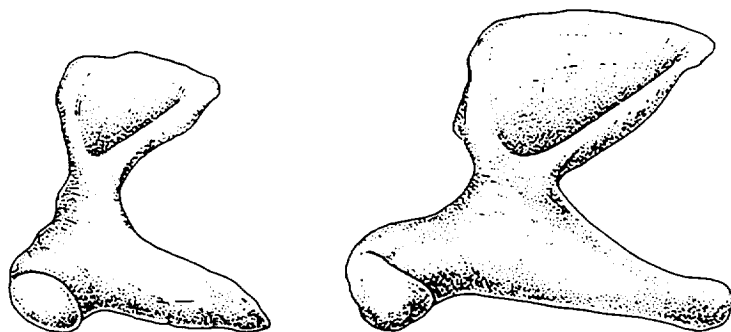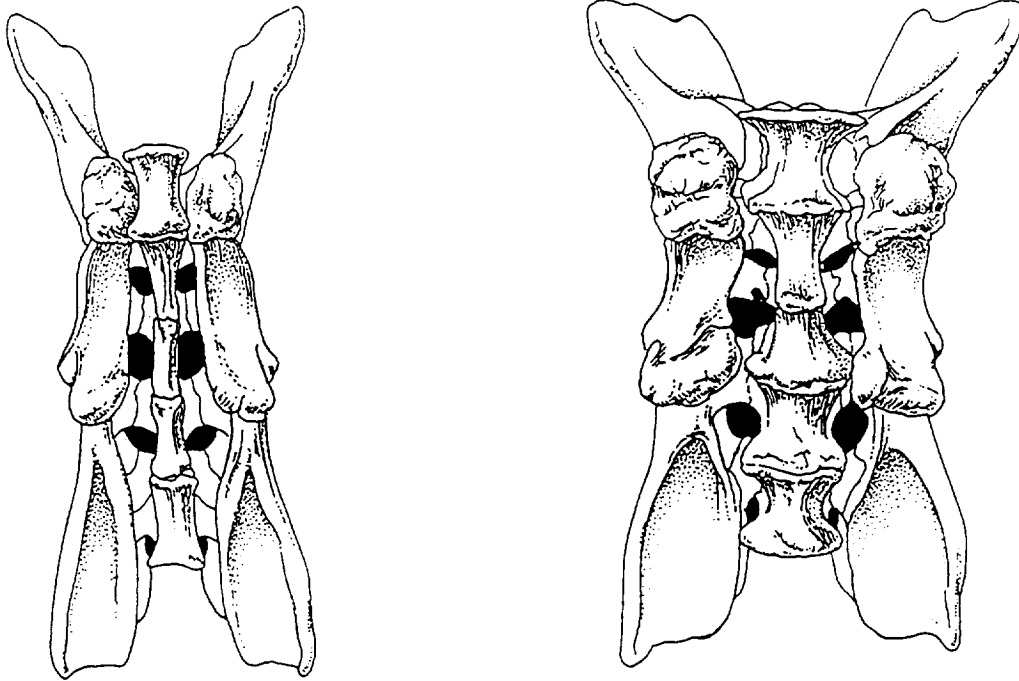
Figure 8

Gracile Morphotype
Robust Morphotype

Tyrannosaurus rex - Pelvis (Sacrum & Ilia) - Ventral View

Illustration: Dorothy Sigler Norton
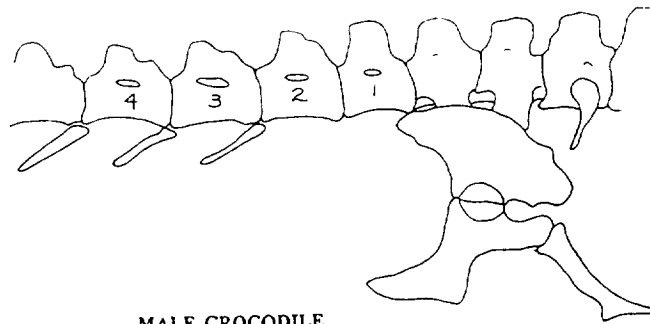
MALE CROCODILE
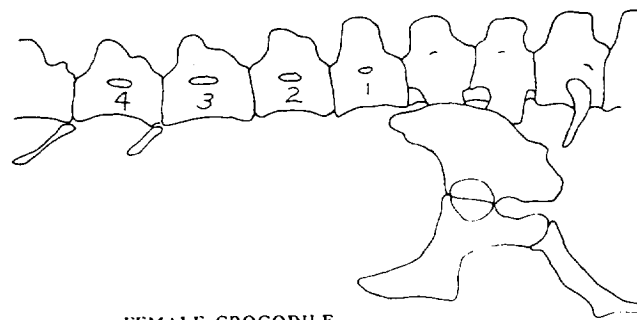
FEMALE CROCODILE

Figure 9

invariably larger than their male counterparts? In fact, they have even coined a male-mammal-chauvinistic term for this phenomenon. They call it "Reversed Sexual Dimorphism".

I suppose that we, as mammals, tend to see everything through "hair-shaded eyes". After all, in mammals, are not the males of a species always (or at least usually) larger than the females? If we look at the animal kingdom as a whole, however, we see quite a different picture. Many species demonstrate this "Reversed Sexual Dimorphism". For invertebrates, the female black-widow spider, who eats her smaller mate after copulation, is the rule rather than the exception. The vast majority of invertebrate species follow a pattern of "Reversed Sexual Dimorphism".

But what about vertebrates? Surely males must be the dominant gender and thus the larger of the species. In fact, we find that in most species of fishes and amphibians, females outsize males. Even in reptiles, most turtle and snake species exhibit "Reversed Sexual Dimorphism". It is really only in mammals that males generally outsize females. But even here, the last stronghold of our prejudice, there are notable exceptions. Female Mysticetes (baleen whales), for instance, are always larger than their male counterparts. Perhaps we should consider referring to the phenomenon of size differences in the sexes simply as: "sexual dimorphism", and be careful about making a judgment as to what is "normal" and what is "reversed".

And what, indeed, is normal? Because ornithologists have assumed that males are "normally" larger than females they struggle with the question of why female raptors are larger than males. Countless papers have proposed complex theories to try to explain a process of natural selection which could produce this "unnatural" result. But what if it is not "normal" for the male to be the larger of the two sexes? What if the "normal" situation is for the female to be the more "robust", as seems to be the case with most species?

Consider, if you will, the act of sex for the procreation of life. Male and female each bring to this union one half of the genetic material necessary for the creation of a new being. The male brings his half of the genes in a conveniently tiny package called a sperm cell, which he produces by the millions. The female, however, not only brings her half of the genes but she also must provide a very large bundle of nutrients encased in a huge package called an egg. She is born with a set number of eggs that she releases throughout her lifetime. Not only does this mandate that she invest more energy into the nurturing of these "tickets to eternity" but that the size of her body should, necessarily, be larger than her male counterpart.

If it is "normal" for the female to be the larger of the two sexes, then all we need to do is use natural selection and competition between males to explain why males sometimes become larger than females. A larger male has a distinct advantage in combat. To the winner go the spoils and thus the propagation of larger and larger male size. This condition is best displayed in herding mammals where a dominant male fights off smaller males for the right to impregnate multiple females.

Why don't we see this condition in birds of prey? Raptors, and other species of birds where females are larger than males, all have one thing in common: **They are monogamous.** Monogamy, and a one-to-one ratio between males and females, does not require competition between males for the right to impregnate multiple females. Thus, female birds of prey are larger than males.

Were female theropods larger than males? Certainly when we look at birds of prey we reach the conclusion that they <u>could</u> have been. And if they were monogamous, females probably were larger than males.

CROCODILES

Paleontologists have often used crocodiles as models for dinosaur behavior. They are used as models because they have many shared characters with dinosaurs and presumably share a common ancestor. Thus, if we could find a skeletal character which defines the sex of an individual crocodile, we may be able to find this same character in dinosaurs.

Eberhard Frey, a colleague from Karlsruhe, Germany, has long studied crocodiles. During the course of his investigations he has performed many dissections. Through his dissections of the reproductive organs, he has recorded some important information. He has also made a remarkable discovery.

In crocodiles, sexual reproduction and removal of waste are all performed through one opening called the cloaca. Male crocodiles have an intromittent organ as do snakes, turtles, and some birds. This "penis" apparatus has a slightly different construction than a mammalian penis, although its function is similar. Unlike mammals, who have an external penis, the crocodile "penis" is retracted when not in use, past the cloaca and into the body. To retract and protect this organ, a "penis-retractor muscle" is necessary. Frey found that in crocodiles this muscle is anchored to the first chevron, or haemal arch. Chevrons are the bony spines attached to the base of the tail (caudal) vertebrae.

Frey discovered that the first chevron in male crocodiles is approximately the same size as the second presumably to give more surface area for the attachment of this muscle. In contrast, the first chevron of female crocodiles is only one-half the size of the second. The position and size of this first chevron would logically provide more room for the female's delivery of eggs.

In addition, what we have found through our own examinations is that this first chevron is attached to the rear of the second caudal vertebra in males and to the rear of the third caudal vertebra in females (Fig. 9). Interestingly, A. Romer noted this dichotomy back in 1956. Unfortunately, it was not linked to sexual dimorphism and the significance of this character went unnoticed. Finally, we have a sexually related skeletal character based upon the presence or absence of a specific sexual organ.

We may use this same sexually related skeletal character in dinosaurs, particularly in theropods like *Tyrannosaurus rex*. It seems that we have this dichotomy of first chevron size differentiation in some mounted skeletons and that researchers have noted that the first chevron occurs on different caudal vertebrae in some specimens which have been assigned to the same species. Unfortunately most descriptive work and restorations were done years ago. In most cases we do not have detailed notes or photographs to assure us that what was mounted and restored represents the condition of the living dinosaur. Chevrons are only attached to the vertebrae by ligaments and are very easily disarticulated as the flesh is decomposed although the caudal vertebrae will usually show an articulation that demonstrates the presence of a chevron. So, we must concentrate our search on newly discovered, undisturbed or well documented materials. Therefore, I made a plea, in October of 1992 at the annual meeting of the Society of Vertebrate Paleontology, for help in locating suitable specimens.

In the summer of 1993, Dr. Philip Currie from the Royal Tyrrell Museum in Drumheller, Alberta, located just the material we had been looking for (personal communication). For several years he has been preparing and examining *Saurornithoides* and other troodontids from China. Troodontids are theropods closely related to *Tyrannosaurus*. Like *Tyrannosaurus*, *Saurornithoides* may be divided into "robust" and "gracile" morphotypes. Dr. Currie has prepared articulated specimens of each form. After listening to my plea he carefully examined the chevrons at the base of the tails of these specimens. He found that in the "gracile" form, the first chevron is positioned on the front of the first caudal vertebrae (on the rear of the last "sacral" vertebrae) and is approximately the same size and shape as the second. The first chevron on the "robust" form is positioned on the rear of the first caudal vertebrae and is more wedge-shaped and shorter than the second. Thus, these skeletons demonstrate that the "robust" and "gracile" morphotypes are indeed separable on
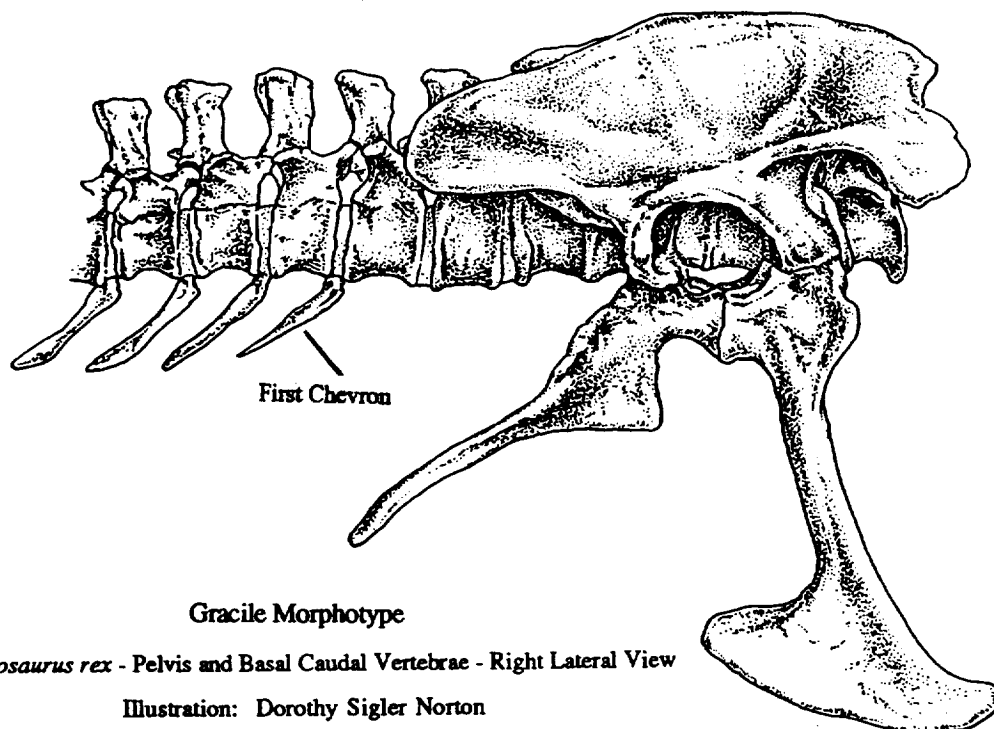
Gracile Morphotype

Tyrannosaurus rex - Pelvis and Basal Caudal Vertebrae - Right Lateral View

Illustration: Dorothy Sigler Norton
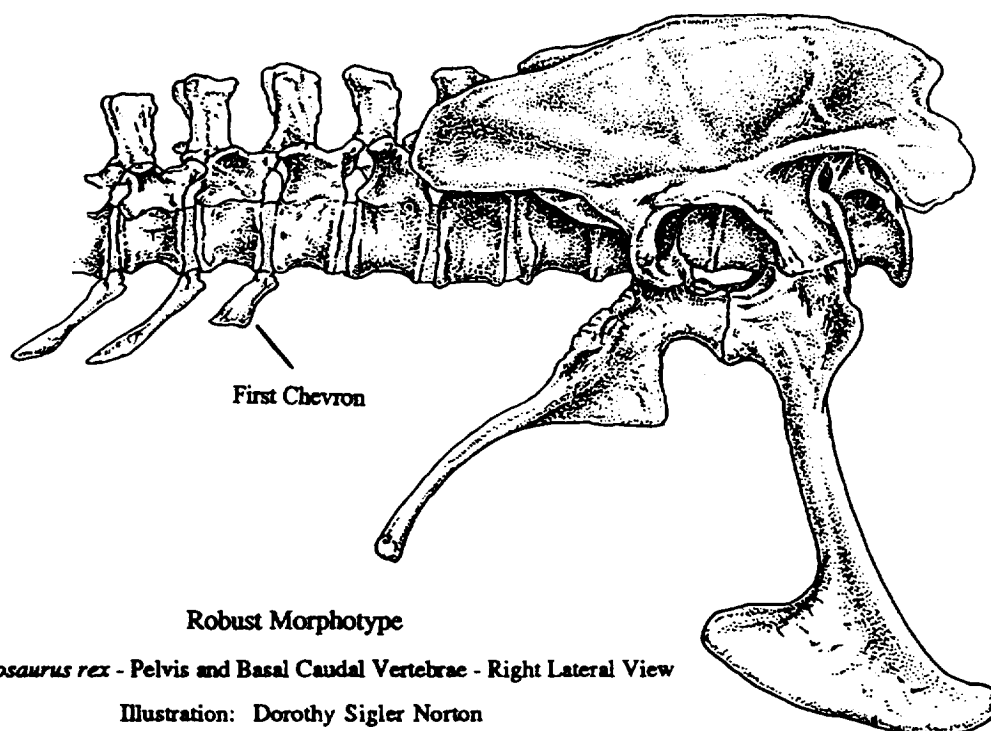
Robust Morphotype

Tyrannosaurus rex - Pelvis and Basal Caudal Vertebrae - Right Lateral View

Illustration: Dorothy Sigler Norton

Figure 10

the basis of skeletal characters defined by the sex of the individual. My conclusion is that, in this theropod, "gracile" morphotypes are male and "robust" morphotypes are female.

An examination of *Tyrannosaurus rex* seems to yield the same result. In the partially articulated gracile specimen at the Museum of the Rockies (MOR-555), the first and second chevrons are the same length and roughly the same shape. Although we cannot check SUE™ because she is locked away from view, it is reasonable to assume that we may reconstruct a parallel with *Saurornithoides* (Fig. 10). This would place "robust" morphotypes, like SUE™, into the female gender and MOR-555 into the male. Although these results may work for theropods, it would be presumptuous to automatically assume that they work for all dinosaurs. In fact, preliminary surveys indicate that the opposite assignment may result for ornithopods like the herd-dwelling hadrosaur *Edmontosaurus annectens* whose social behavior may parallel mammalian harem habits.

CONCLUSION

There have been fifteen significant specimens of *Tyrannosaurus rex* discovered to date. These specimens may be divided into two groups or forms: a "robust" morphotype and a "gracile" morphotype. By comparison with birds and crocodiles, the closest living relatives of dinosaurs, it seems clear that these morphotypes represent sexual differentiation. By observing which vertebra bears the first chevron, as well as the shape and size of that chevron, we are able to "sex" individual skeletons. Results of these observations indicate that, for *Tyrannosaurus rex* and other theropods, the "robust" morphotype is female and the "gracile" morphotype is male. The identification of this anatomical character could help to clear up confusion which may have resulted in the description of male and female as different species. It also follows that male *Tyrannosaurus rex* (and other dinosaurs) had an intromittent organ or "penis" similar to crocodiles and some birds. But most unexpectedly, I believe that in all probability *Tyrannosaurus rex* was monogamous and probably maintained family groups.*

Now that we have seemingly found a method of determining the gender of specific dinosaur skeletons, we should be able to attribute isolated robust or gracile elements to a specific sex. We should then be able to use this information together with taphonomic, stratigraphic and geographic data to help bring to life the behavior of animals extinct for 65 million years.

*Additional data which supports the "family group" hypothesis was found with SUE™. During her excavation and preparation we discovered fragmentary remains of a smaller adult male, a juvenile and an

infant *Tyrannosaurus rex*. During the course of this study it was also noted that the adult male skeleton (LACM-28344) and a juvenile skeleton (LACM-28345) of *Tyrannosaurus rex* reposited at the Los Angeles County Museum of Natural History were found together in the same excavation.

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Steak Knives, Beady Eyes, and Tiny Little Arms
(A Portrait of *T. rex* as a Scavenger)

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I'll begin with the obvious question, how many people saw the movie "Jurassic Park"? How many people believed it? In the movie, "Jurassic Park", there were basically two stars. *Tyrannosaurus rex* was one of them and the *Velociraptors* (or *Deinonychus*, or whatever they happened to be) were the others. What you might also know is that I was an advisor on the movie. All I was able to do was basically tell them when the dinosaurs were walking right and tell Laura Dern how to pronounce her words.

Any time the dinosaurs were going to do something, any time Steven Spielberg wanted to have the dinosaurs do something in the movie, he would ask me if I thought they could do that. If I said yes or no, he would take that as an answer. But if I said maybe, he would just do whatever he wanted. That's fiction.

Tyrannosaurus rex, in the movie, is portrayed as a jeep chaser and a tire chewer. He also spent a lot of time chasing people around. I would like to convince you that he wouldn't have done that. In fact, I think the only thing that *Tyrannosaurus rex* would have done in that movie is eat that lawyer.

Another imaginative picture of *T. rex* which we've already seen is on the jacket of a very famous book, but I can't remember its name. It has *Tyrannosaurus rex* doing something (it's unclear exactly what), some kind of a dance of some sort, with this other dinosaur. I'm not sure exactly what the other dinosaur is supposed to be, but if this is *Tyrannosaurus rex,* then obviously, it is a new horned dinosaur. On the other hand, if the horned dinosaur is *Styracosaurus,* then the carnivorous dinosaur is not *Tyrannosaurus rex.* But it is supposed to be.

I have, on several occasions, suggested that tyrannosaurs may be scavengers. And so if I may, let's talk about *Tyrannosaurus rex.*
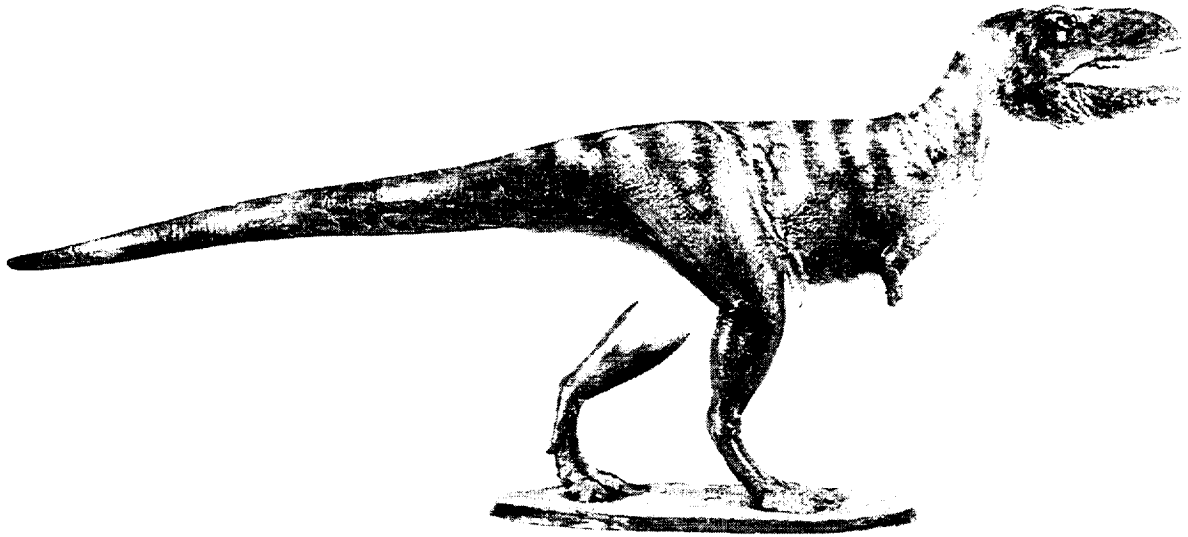
Figure 1. *Tyrannosaurus rex*. Photo courtesy Museum of the Rockies, Montana State University, Bozeman.

    Tyrannosaurus rex was first found in 1902 by Barnum Brown. Henry Fairfield Osborn named it the "tyrant lizard king". When Brown found the first one, he brought it back to New York and put it together in a particular pose which, as we all know now, is wrong. But the American Museum of Natural History has a very high ceiling. They needed to get as high in that empty space as possible, so they broke the tail and stood it up as high as they could get it. Of course, they had to break a few other things on the way. The whole idea here was to make *Tyrannosaurus rex* look mean. It was assumed from the time it was found that it was, in fact, a predator. I don't think it was.

    There are a number of different kinds of tyrannosaurs: there's *Tyrannosaurus rex, Daspletosaurus, Allosaurus, Albertosaurus*, and a little thing called *Tarbosaurus* from Mongolia. All of them share a bunch of characters. They all have short little front arms, are relatively large (Figure 1) and have this incredible mouth full of teeth (Figure 2). Together we call them all tyrannosaurs. That's really what this talk is about, tyrannosaurs in general. And, as I was saying, they are famous for mouths full of teeth.

    As I've said before, paleontology should be fun. I think it also has to make sense. We have to have some common sense thrown in here. So, we start with the very basics: what did *Tyrannosaurus* eat? We've heard that

tyrannosaurs eat meat and in "Jurassic Park", a lawyer, which is meat I guess, dark meat probably. The teeth of tyrannosaurs, of all the tyrannosaurs, are pointed. They have serrations on the front and back, like steak knives. *Tyrannosaurus* had a mouth full of steak knives. If they had a mouth full of steak knives, then obviously, they ate meat. But just looking at the teeth doesn't really prove anything. We really have to look at bone that has puncture marks, such as a portion of the pelvis of a *Triceratops* that I've studied. The punctures, we believe, were made by a tyrannosaur. We gather this from some of the striations which appear to be caused by the serrations actually sliding across the bone. We have other bones such as a fibula, or lower leg bone, of a duckbill. There is a long gouge in the bone and a puncture. Down inside the bone, we found the tip end of a tyrannosaur tooth. From bones like these, there's no question tyrannosaurs were actually chewing on dinosaurs. The question is whether the dinosaurs were actually alive when *Tyrannosaurus* did that.

In 1990, we found what everyone is now claiming is the second most complete *Tyrannosaurus rex* skeleton. Basically, what we did was excavate it and prepare it. Then we figured out where the muscles would go on it and then we made a model of the animal. Jim Farlow and Matt Smith took the completed model and dunked it in water to figure out how much it would weigh and estimated it at about 40 feet long and 12,000 pounds. The interesting thing about this particular specimen is, even though it may be only the second most complete one, it had the first complete arm. And from that arm, Matt Smith looked at the muscle scars on it and figured out where the muscles would go and kind of fleshed it out and it looks like sort of an Arnold Schwarzenegger arm. *Tyrannosaurus rex*, 40 feet long and weighing 12,000 pounds, has an arm exactly the same length as mine from the shoulder blade to the end of the fingers. I'm sure most of you have seen or read some of the ideas of what tyrannosaurs did with their arms and, of course, there was the theory proposed that *Tyrannosaurus* got down on its hind legs, sat down on the ground, and then needed these arms to help him get up off the ground. This is where common sense comes in. Does that make sense? Pack it in muscle and there was only part of the arm left actually sticking out from the body. It was capable of about three inches of rotation at the elbow and even less at its wrist. So here we have an animal that had these two tiny little front legs or arms that will not come together. He cannot bring his two arms together. I don't know what *Tyrannosaurus rex* did do with those arms, but I don't think he used them to get up off the ground. In fact, I'd say the only thing he did was maybe scratch his belly after a good meal. Unfortunately, I don't think he had many good meals.

Arms obviously are very important if you're a predator. I'm not saying all predators use their front legs, but most of them do. A lion uses its front legs to capture a zebra. People who try to make *Tyrannosaurus rex* a predator have to come up with some pretty elaborate schemes in order for *Tyrannosaurus rex* to actually catch his prey. Use your imagination here, think about how much sense it would make. Think about a *Triceratops*

running down the street, and a *Tyrannosaurus rex* running along behind it. *Tyrannosaurus rex* has to catch this thing, but he doesn't have any arms. To put this in perspective, imagine yourself running down the street, holding your arms behind your back and you're after something like a chicken. It has been suggested that *Tyrannosaurus* just ran right up beside *Triceratops*, or whatever it was after, and kicked him over. Can you imagine yourself running up next to that chicken and just kicking it over?

It has also been suggested that tyrannosaurs ran ahead of their prey and then knocked them over with their tails. We know that *Triceratops* wasn't very smart, but I feel fairly sure it was smart enough to know when *Tyrannosaurus rex* was running just ahead of it.

Front legs are really important for a predator to be able to stabilize its prey, to grab ahold of it and keep it still long enough to bite it. Otherwise, if we assume that the *Triceratops* doesn't want to get caught, when it does, it's going to shake around a lot. *Tyrannosaurus* has big teeth, but I just cannot imagine that *Triceratops* doing all that shaking around in the mouth would do the *Tyrannosaurus'* mouth any good, let alone the teeth. So this is where I have a problem with common sense. I don't think *Tyrannosaurus rex* could catch a *Triceratops*, certainly not with its mouth.

Living at the same time as *Tyrannosaurus* were a whole bunch of other interesting animals that we know were predators. *Troodon* is a very good example. *Troodon* was not very big, standing maybe about four or five feet tall. But it has good grasping arms. It has lots of rotation at its elbows and rotation at its wrists. There were other animals, such as *Deinonychus* , which really didn't live at the same time but it was closely related to *Velociraptor* , as John Ostrom has pointed out. It also had good grasping arms with lots of rotation.

From looking at the specimen that Don Lessem showed us, we know that animals such as *Velociraptors* used their hands . The *Velociraptor* is laying on its back and locked with a *Protoceratops.* You can clearly see the left arm coming up and around. The left hand, the claw, is on one side of the *Protoceratops* ' skull and his right arm goes around the other side and the hind legs come up and both killing claws are buried in the chest area of the *Protoceratops* . This is a very good example showing that *Velociraptor* is a predatory dinosaur and he's using his hands. *Tyrannosaurus rex* couldn't do that.

We could certainly argue about this, but if we look at the predatory dinosaurs, we find that they all have a short femur and a long tibia. In other words, they have a long shin bone and a short thigh bone. This holds true for things like *Troodon* , the *Velociraptor* , and *Deinonychus* . We know of many bipedal animals that have this long tibia and short femur; living ones like ostriches or ratites, any of the ground birds, like rheas, emus, cassowaries and so on. Rheas, animals like that, are about the same size as

we are. Their legs are about the same length as ours, but they have a short femur and a long tibia. Ever tried to catch a bird like this? You can't catch one. We can't catch one because we have a femur and a tibia that are the same length and that's not good for running. In fact, when we have a human race, we're basically trying to find out how fast a really slow, big animal can go. And here we have another animal, *Tyrannosaurus rex* or any of the tyrannosaurs, that has a femur and a tibia the same length, just like ours. It doesn't look like they could go very fast either, certainly not comparable to the animals with good grasping arms.

Figure 2. Model of the skull of *Tyrannosaurus rex*. Photo courtesy Museum of the Rockies, Montana State University, Bozeman.

There are a lot of other things about tyrannosaurs that are sort of interesting. I don't know what it means, but if you look at the skull (Figure 2), you will see these little openings where the eyes go, so it looks like it has beady, little eyes. The *Troodon* and *Velociraptor* and things like that had big eyes. I don't know if that means anything or not. It's also interesting to look at the brain case of tyrannosaurs. We find a very large olfactory lobe, the part of the brain used for the sense of smell. I don't know if that's worth anything, either.

What is interesting is where we find tyrannosaur remains; not where we find their skeletons, but where we find some of their other remains. And

for this we have to look at my favorite dinosaurs. By the way, even though I've coauthored two books on *Tyrannosaurus rex*, it is my least favorite dinosaur.

Eighty million years ago up until about 65 million years ago, there was an intercontinental seaway extending from the Gulf of Mexico to the Arctic Ocean, separating North America into the two parts they're socially separated into now. There were the Rocky Mountains in western North America and extending out from the Rocky Mountains down to the seaway was a broad coastal plain. Work being done now on this area, looking at the sediments and vegetation, suggests that there was a lot of vegetation along the river courses, but there wasn't a lot in between. It must have been like plains with bushes and maybe some ferns and things like that, but not the jungle we usually picture in this part of the world at that time.

Over the years we have found evidence of nesting grounds and a lot of other things that show that the hadrosaurs, the duckbills, were social animals. They actually nested in some kind of colony or aggregation. So we can say that these dinosaurs were social and we have very good evidence that they were. After these dinosaurs left their nesting grounds, we have pretty good evidence that they were still social. A lot of this comes from these bone beds that we find. One of the better ones we've found over the course of several years is named the campasaur pit because it's in our camp. Fortunately, we found it a couple of years after we started camping there. Anyway, the campasaur pit is about 100 feet long and 30 feet wide and out of that, we have taken about 60 skeletons, or at least parts of 60 skeletons. The area that this bone bed encompassess is about four miles long and about a quarter of a mile wide and everywhere on that area that we've ever dug a test pit, we've found about 30 bones per square meter. There are thousands of individuals there. In fact, we estimate, based on 30 bones per square meter, there were somewhere around 10,000 to 15,000 animals that died there. They are encased in volcanic ash and mudstone and it appears that these dinosaurs died in some sort of catastrophic volcanic event. All of the skeletons that we find are maiasaurs, plant-eating dinosaurs, relatively large and from the fact that they died in what appears to be a catastrophic event, it appears that they lived together in some sort of social group. And since they were plant-eating, they probably travelled, moving from one area to another.

In another area, about 60 miles north of the campasaur pit, we have found another gigantic bone bed that contains the bones of a duckbilled dinosaur called *Parasaurolophus*. One or two thousand individuals appear to have died in some sort of flood related event, maybe a flooding stream or something like that. At another site in another area, we find the remains of a duckbilled dinosaur called *Hypacrosaurus* in another gigantic bone bed where we have at least several hundred individuals, if not a couple of thousand. All of this evidence plus the giant bone beds found in South Dakota, other parts of Montana, and in southern Canada suggest that all of

the duckbilled dinosaurs did live in groups, or possibly at least, in some sort of social groups.

There are also indications from some other bone beds where we have thousands of individual horned dinosaurs. *Styracosaurus* beds have been found in Canada. *Pachyrhinosaurus, Centrosaurus* and what appears to be *Triceratops* bone beds have also been discovered. These all suggest that the horned dinosaurs also lived in gigantic herds.

If we find a styracosaur bone bed, it is almost all *Styracosaurus*. Sometimes there's other stuff mixed in with it, but 90% will be of the same species. In some instances, in fact in all of the bone beds, whether it be the horned dinosaurs or the duckbilled dinosaurs, whatever it is, mixed in with the skeletal remains we find an abundance, and I do mean an abundance, of tyrannosaur teeth. Not an abundance of *Velociraptor* teeth or an abundance of *Troodon* teeth, but an abundance of tyrannosaur teeth. Dinosaurs, like crocodiles living today, replaced their teeth throughout their lives. If a tooth was broken, the dinosaur would simply grow a new one. We find that tyrannosaur teeth are very, very common in these bone beds. This suggests, I would say, that these dinosaurs, the tyrannosaurs, were doing something with these dead animals.

Look at a possibly comparable situation, the giant herds of wildebeests in the Serengeti plain of Africa. Wildebeests travel in gigantic groups from one area to another. They herd, they migrate. And when they migrate and they come to obstacles such as water, they cross them regardless of what's going on. If the river is in flood, they will keep going, not because they are stupid, but because there are another million of them coming behind and there's nowhere else to go.

There are millions of wildebeest in these herds. In the course of a single migration, an annual migration, they can loose up to 200,000 individuals. 200,000 of them can die in a single migration. A lot of them die in events such as floods, a lot of them die in drought situations. And I suspect that if they were walking along next to a volcano, then they would probably die in volcanic ash as well. What you end up with is a whole lot of meat.

I'm sure most of you know that predatory animals get their prey about one time in every ten. That means nine of those tries are misses. Scavengers are better. They can get their's every single time. It's not going anywhere and the longer it sits there, the easier it is to find. You just can't be too picky.

Following these giant herds are the scavengers. Obviously there are a lot of animals that feed on these carcasses. Picture *Tyrannosaurus rex*. He has no arms, can't run fast, appears to have a large olfactory lobe and he's big. Interestingly enough if you think about it, one of the best things to be if

you are a scavenger is big so you can chase away anything else around the carcass.

It might be a horrible thing to think about, but we are scavengers too. We just get our meat in a nice, neat little package at the Safeway store. Scavenging, I think, is probably very specialized and it is the kind of thing that you would find associated only with large herds of individuals. For all these reasons, I think the *Tyrannosaurus rex* was a scavenger and since it's almost 11 p.m., I hope no one wants to argue with that. Thank you.

Wear Surfaces on the Teeth of Tyrannosaurs

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INTRODUCTION

Large theropod dinosaurs like tyrannosaurs were the biggest land-living predators in earth history. Because of this, there has been considerable interest in reconstructing the paleobiology of these immense carnivores (Bakker, 1986; Bakker et al., 1988; Paul, 1988; Molnar and Farlow, 1990; Farlow et al., 1991; Abler, 1992; Farlow, 1993, in press; Horner and Lessem, 1993). In the present paper we consider a topic relevant to interpretations of how tyrannosaurs used their teeth during feeding: the incidence of wear surfaces on tyrannosaur teeth.

MATERIALS AND METHODS

Like other reptiles, carnivorous dinosaurs shed old, worn or broken teeth and replaced them with new, unworn teeth throughout their lives. Consequently isolated theropod teeth are found much more often than theropod skeletons in dinosaur-bearing rock formations.

In the course of a study (Farlow et al., 1991) of overall tooth shape and of the serrated front and rear cutting edges (keels) of theropod lateral teeth (teeth from the sides of the upper [maxilla] or lower [dentary] jaw), we noted the location and severity of various kinds of tooth wear that we observed. This information was combined with more casual observations of wear surfaces on incisor-like teeth from the front of the upper (premaxillary) and lower (anterior dentary) jaws. We also noted the location and severity of wear on unshed teeth in several museum specimens of tyrannosaur jaws.

Our most careful observations were made on a sample of 279 shed lateral teeth from the Late Cretaceous Judith River Formation of western Canada. The great majority of these teeth belonged to tyrannosaurs, but some of the smaller teeth probably came from other kinds of theropods. Although we cannot with certainty identify which species of tyrannosaur was (were) responsible for the shed teeth we studied, most of them appeared to belong to the animal presently known as *Albertosaurus libratus*, and a smaller number to the form presently known as *Daspletosaurus torosus*; we describe these as the "present" names applied to these

dinosaurs because the nomenclature of tyrannosaurid dinosaurs is now in a state of flux, and it may be a while before there is agreement regarding the appropriate names for these reptiles.

We counted the number of teeth in our sample that occurred in each of 4 somewhat subjective wear classes: 1) teeth with little or no wear; 2) teeth exhibiting slight to moderate wear; 3) teeth showing extensive wear; 4) teeth whose wear could not be determined due to poor preservation or post-shedding breakage.

We also tabulated tooth wear in terms of where on the tooth it occurred: at the tooth tip, or on the distal (toward the tooth tip) or proximal (toward the tooth base) half of the serrated keel on the anterior or posterior edge of the tooth, or on the inner (medial/lingual) or outer (lateral/labial) face of the tooth (see Figure 1 for an illustration of these location terms). Our tabulation of the sites of wear in the Judith River tooth sample may be somewhat inaccurate due to the completeness and quality of preservation of teeth. For example, we obviously could not determine the degree of toothtip or distal serration keel wear on teeth whose tips had broken off. However, we think that our data accurately indicate at least the relative frequencies of different sites of tooth wear.

RESULTS

Fifty-eight of the 279 teeth in our Judith River Formation sample exhibited little or no wear (Figure 1). The wear that did occur usually consisted of a few worn or chipped serrations that occurred at the very tooth tip and/or along the serrated keels. Some of this mild wear might even be stream or other abrasion that occurred after teeth were shed, and thus have no significance for interpreting how the teeth were used by the living dinosaur.

Eighty-three of the teeth in our sample showed what we characterized as slight to moderate wear. This wear was located at the tooth tip, or extending a short distance (less than half the length of the keel) from the tooth tip toward the tooth base, along the anterior (Figure 2) or posterior serrated keel, or along the sides of the tooth (with the wear surface covering less than half the length of the tooth).

Eighty-seven of our teeth had what we described as extensive wear (Figures 3-4). This was usually heaviest at the tooth tip, with worn surfaces extending all or most (greater than half the length of the keel) of the way along one or both serrated keels toward the tooth base. The individual serrations were commonly worn flat. Heavy wear also occurred in the form of nearly flat surfaces on the inner or outer sides of the tooth (covering more than half the length of the tooth); the largest such wear surfaces occurred on the inner sides of teeth (Figure 3). The most severe wear occurred on teeth that seemed to have broken while still in the dinosaur's mouth, after which the shattered edges were worn smooth; such teeth had irregular gouges,
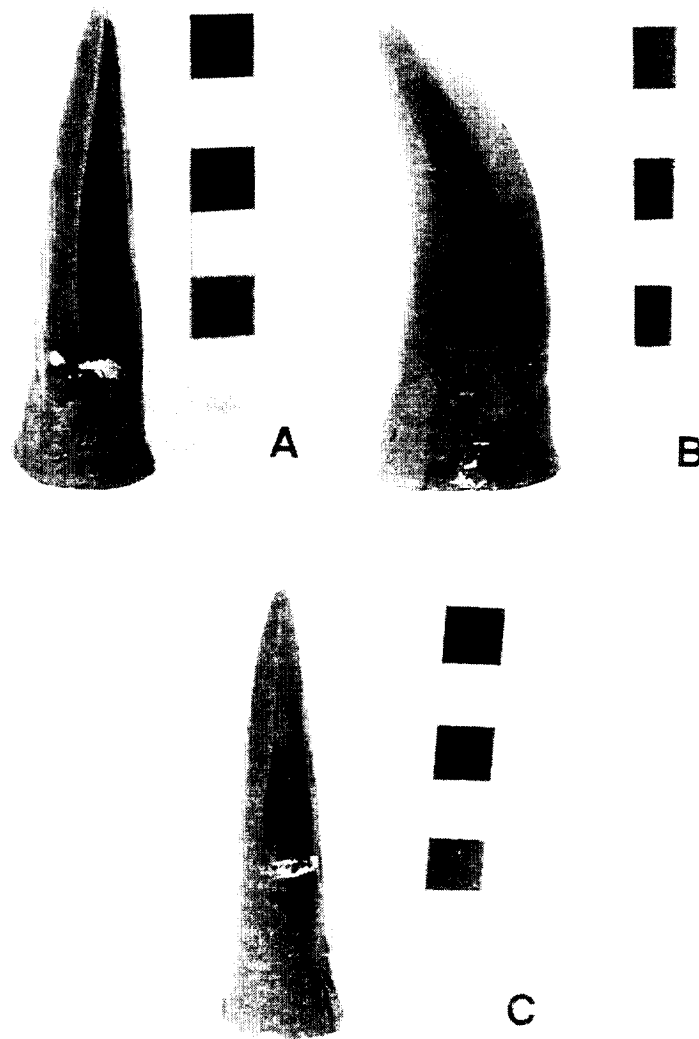
Figure *1*--Cast of a very well preserved tyrannosaur lateral tooth (Yale Peabody Museum [Princeton University] 21848) from the Judith River Formation. This tooth shows little or no wear. The tooth is about 55 millimeters long. The distal end (toward the tooth tip) of the tooth is up and the proximal end (toward the tooth base) is down. *A*, posterior view, lateral (labial) side to the left, and medial (lingual) side to the right; note that the posterior serrated keel is near the outer edge of the tooth (the outer edge is visible as a highlight near the tooth base, on its left side). Cast made by Rob Allen. In this and other photographs, the black and white bars in the scale are each 10 millimeters long; *B*, medial view, anterior serrated keel to the right, and posterior serrated keel to the left; note slightly recurved tooth tip, and that the posterior keel extends farther toward the base of the tooth than the anterior keel does; *C*, anterior view, medial side to the left, and lateral side to the right; note anterior serrated keel.
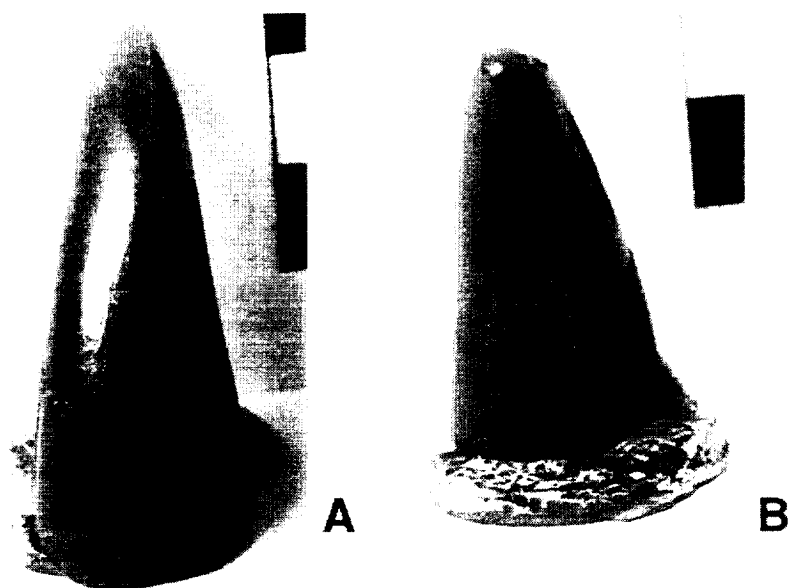
Figure 2--Cast of Royal Tyrrell Museum of Palaeontology specimen number PMA 65-16-133. Tooth length about 38 mm. *A*, anterior view, showing flatworn anterior serration keel at tooth tip; the wear surface laps onto the lateral (outer) tooth face; medial (inner) side of tooth to the right; *B*, posterior view, showing flatworn distal end of posterior serration keel; outer (lateral) tooth side to the right. Cast made by Keith Rigby.

Figure 3--Medial (lingual) view of Royal Tyrrell Museum of Palaeontology specimen number P79.14.796; anterior edge of tooth to the left. Tooth length about 42 mm. Note large, nearly flat wear surface on medial tooth face.
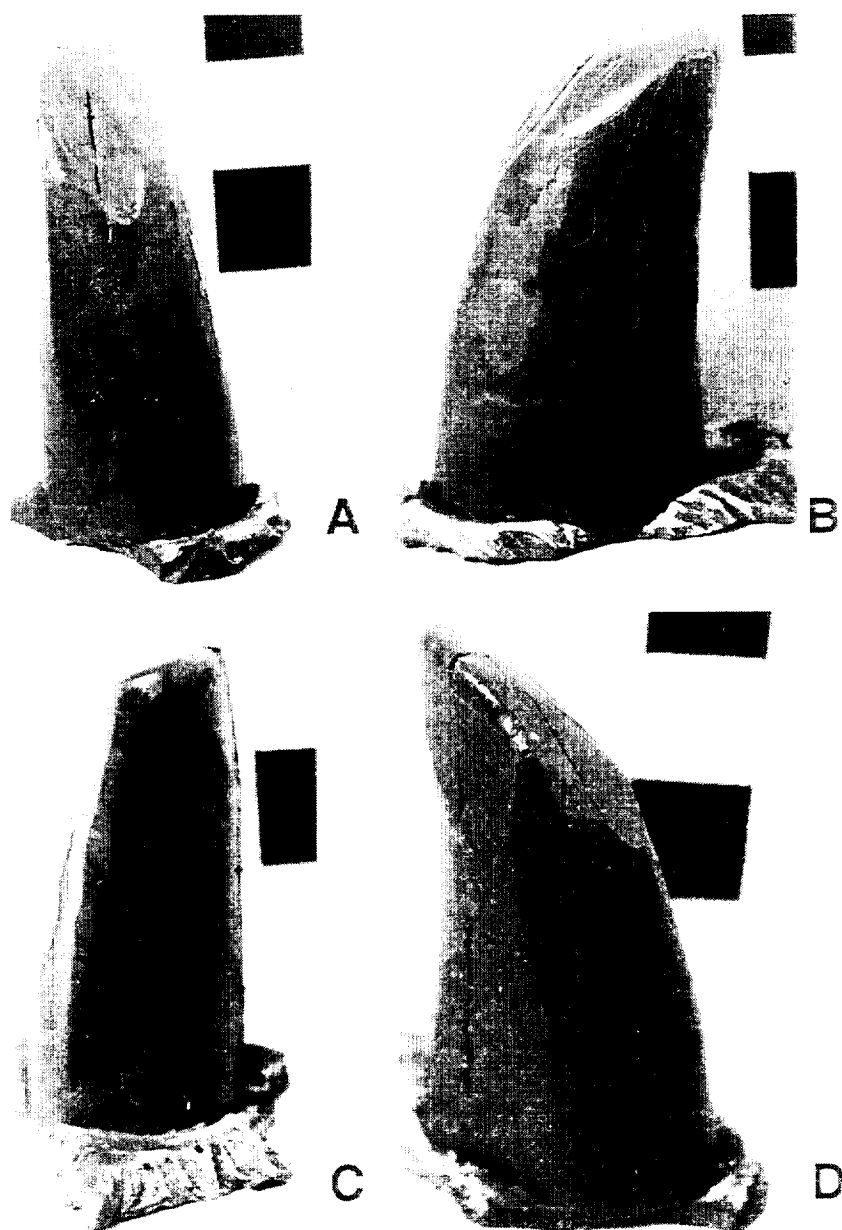
Figure 4--Cast of Royal Tyrrell Museum of Palaeontology specimen number P66.11.94. Tooth length (as preserved) about 42 mm. A, anterior view, medial (inner) tooth surface to the left; B, lateral view, anterior edge of tooth to the left; C, posterior view, medial tooth surface to the right; D, medial and slightly anterior view; what is left of the anterior keel is toward the viewer. The severity of wear of the tooth tip indicates that the tooth broke while still in the tyrannosaur's jaw, after which the broken edges were worn smooth. Cast made by Keith Rigby.

grooves, and tongue-shaped depressions, with smooth edges, near their terminal ends (Figure 4).

We were unable to characterize the degree of wear of 51 of the teeth in our Judith River sample. This was because the tip of the tooth had broken off after the tooth was shed, or because of other kinds of post-shedding breakage, or extreme weathering, of the tooth.

Wear occurred more frequently on the anterior serrated keel than on the posterior keel, more often on the distal than the proximal end of the tooth, and more often on the inner (medial/lingual) than the outer (lateral/labial) tooth face (Table 1).

Although we did not count the number of occurrences of wear surfaces on the incisor-like teeth of the premaxilla and anterior dentary in our study, we frequently observed wear on the marginal keels of such teeth, as well as on their anterior (labial) and posterior (lingual) faces. A particularly striking wear surface occurs on the anterior face of a premaxillary tooth of the type specimen of *Daspletosaurus torosus* (Canadian Museum of Nature specimen number 8506).

Wear *only* on Tooth Tip	Anterior Keel		Posterior Keel		Inner (Lingual) Face of Tooth		Outer (Labial) Face of Tooth	
	Dist	Prox	Dist	Prox	Dist	Prox	Dist	Prox
16	103	63	41	20	56	25	39	7

TABLE *1*--Location of wear on shed lateral teeth of theropod dinosaurs (mostly, but probably not entirely, tyrannosaurs) from the Judith River Formation of western Canada. The number in each cell of the table is the number of teeth, out of a sample of 170 teeth showing slight to severe wear, that displayed wear in the location represented by the cell. A given tooth could have wear in more than one of the locations represented by the cells of the table (except for teeth in the first column, in which the only wear observed on the tooth was at its very tip). "Dist" indicates that the wear occurred on the distal (toward the tooth tip) half of the tooth; "prox" indicates that the wear occurred on the proximal (toward the tooth base) half of the tooth.

The kinds of wear that we observed in teeth still present in tyrannosaur jaws, were, unsurprisingly, consistent with what we saw in our shed tooth sample. In general, though, the severity of wear on teeth *in situ* in the jaws of tyrannosaur specimens was less than on isolated, shed teeth. This is not very surprising. A given tyrannosaur tooth may have had a "lifespan" of a few years in the jaw before it was shed (G. Erickson, personal communication). We would therefore expect isolated teeth to be, on the average, "older" than teeth still present in the jaws of their owners. Consequently shed teeth are more likely to display wear than teeth still present in the jaws. We suspect that many or most isolated teeth that show little wear (Figure 1) broke away from the jaw prematurely, perhaps during fighting or feeding.

DISCUSSION

The serrated incisor-like and lateral teeth of tyrannosaurs are similar in many respects to their counterparts in other living and extinct predators (Farlow et al., 1991; Abler, 1992). In the present study we wish to draw attention to the similarities among teeth of tyrannosaurs, the modern Komodo dragon or ora (*Varanus komodoensis*), and the upper canine teeth (sabers) of the extinct sabertoothed cat *Smilodon*; similarities between ora teeth and sabercat sabers were previously noted by Akersten (1985). In tyrannosaur and ora lateral teeth, and in the sabers of *Smilodon*, the posterior serrated cutting edges of the teeth are longer than the anterior serrated keels. The proximal end of the anterior cutting edge of a *Smilodon* saber "is noticeably nearer the inner or median side of the tooth" (Merriam and Stock, 1932:48). The same is true for tyrannosaur teeth, particularly those of the Judith River form presently called *Albertosaurus* (cf. Lambe, 1917:17). The distal portion of a tyrannosaur lateral tooth has an oval cross section somewhat like, but less compressed than (Farlow et al., 1991), that of a sabercat saber; the distal cross sectional shape of a tyrannosaur tooth is even more similar to that of an ora.

The base of the exposed (above the jaw line) portion of a sabercat's saber is "quite rounded proximal to the termination of the anterior serrations" (Akersten, 1985:5), while the rear margin of the saber is more compressed. In tyrannosaurs and the ora the base of a lateral tooth has a rather rectangular cross section, and the basal end of the posterior keel is commonly situated at or near the posterior and outer corner of the tooth. Because the posterior keel commonly extends closer to the base of the tooth than the anterior keel does, the tooth base has a blunt anterior face and a serrated posterolateral edge (cf. Bakker, 1986:260-261), making the tooth base something like that of a *Smilodon* saber.

The incisor teeth and the lower jaw canines of *Smilodon* somewhat resemble the incisor-like premaxillary and (to a lesser extent) anteriormost dentary (lower jaw) teeth of tyrannosaurs and the ora. These teeth all have a rounded anterior (labial) portion separated from a flat or slightly convex or concave posterior (lingual) face by

keels or edges, sometimes serrated, on either side of the tooth (cf. Merriam and Stock, 1932; Akersten, 1985).

Given these similarities in tooth form between tyrannosaurs, on the one hand, and sabercats and oras, on the other, it is not unreasonable to expect similarities in the way these carnivores use(d) their teeth during feeding. This in turn would suggest that there should be similarities in wear surfaces on the teeth of these three kinds of predator.

Komodo dragon lateral teeth that we have examined frequently show tooth tip and distal anterior keel wear very like that seen on tyrannosaur lateral teeth. Although wear on *Smilodon* sabers is not common, the tips of some sabers show "moderate to extreme wear of the serrations" (Akersten, 1985:17), and some upper canines (especially of saberkittens) have modest-sized wear facets near the tooth tip (Akersten, 1985). In some individuals of *Smilodon* one or both sabers broke during life and was (were) subsequently worn smooth. One left saber has a large wear facet on its inner side (Akersten, 1985: Figure 9D) that is strikingly similar to the wear surfaces often seen on the inner faces of tyrannosaur teeth. Thus what wear is observed on *Smilodon* sabers is reminiscent of that seen on tyrannosaur lateral teeth. In contrast, the anterior (labial) parts of the tip regions of *Smilodon* incisor teeth do not show wear (Akersten, 1985), unlike the incisor-like anterior teeth of tyrannosaurs.

These observations indicate that interpretations of how tyrannosaurs used their teeth during feeding can be made not only on the basis of study of the dinosaur teeth themselves, but also by judicious comparison with observations of feeding behavior in oras, and interpretations of feeding behavior in sabercats (Auffenberg, 1981; Akersten, 1985; Farlow et al., 1991; Abler, 1992). Drawing on all of this information permits us to construct the following scenario of feeding behavior in tyrannosaurs.

Tyrannosaurs probably made deep bites into their victims (Figure 5), penetrating both soft tissues and bone (Paul, 1988; Molnar and Farlow, 1990; Farlow et al., 1991; Abler, 1992; G. Erickson, personal communication). As the jaws closed, teeth of the upper tooth row passed on the outside of those of the lower jaw. Meat was trapped in spaces between the anterior and posterior serrated keels of adjacent teeth in both the upper and the lower jaws. As the jaws closed the between-tooth spaces of the upper jaw were pushed against those of the lower jaw as teeth from the lower jaw came closer to teeth of the upper jaw. This forced meat against the serrated keels of both upper and lower teeth, cutting it, or perhaps binding it, after which it was torn from the victim by forceful jerks of the tyrannosaur's head (Figure 5).

The greater incidence of wear on the distal than on the proximal portions of the serrated keels of tyrannosaur lateral teeth is not surprising. The tooth tip would have been the first part of the tooth to penetrate the victim, and so the distal parts of teeth were probably subjected to the greatest resistance from the victim's body, prior to

initial rupturing or tearing (or breaking) of soft tissues or bone. Because tyrannosaur teeth are slightly recurved at their tips (Figure 1), the anterior serrated keel probably encountered greater resistance from the victim's body than the posterior keel did, resulting in greater abrasion of the anterior than of the posterior keel, as seen in our data (Table 1). Wear on the posterior keel may also have resulted from stresses created when the tyrannosaur jerked its closed jaws backwards, away from the victim's body (Figure 5).
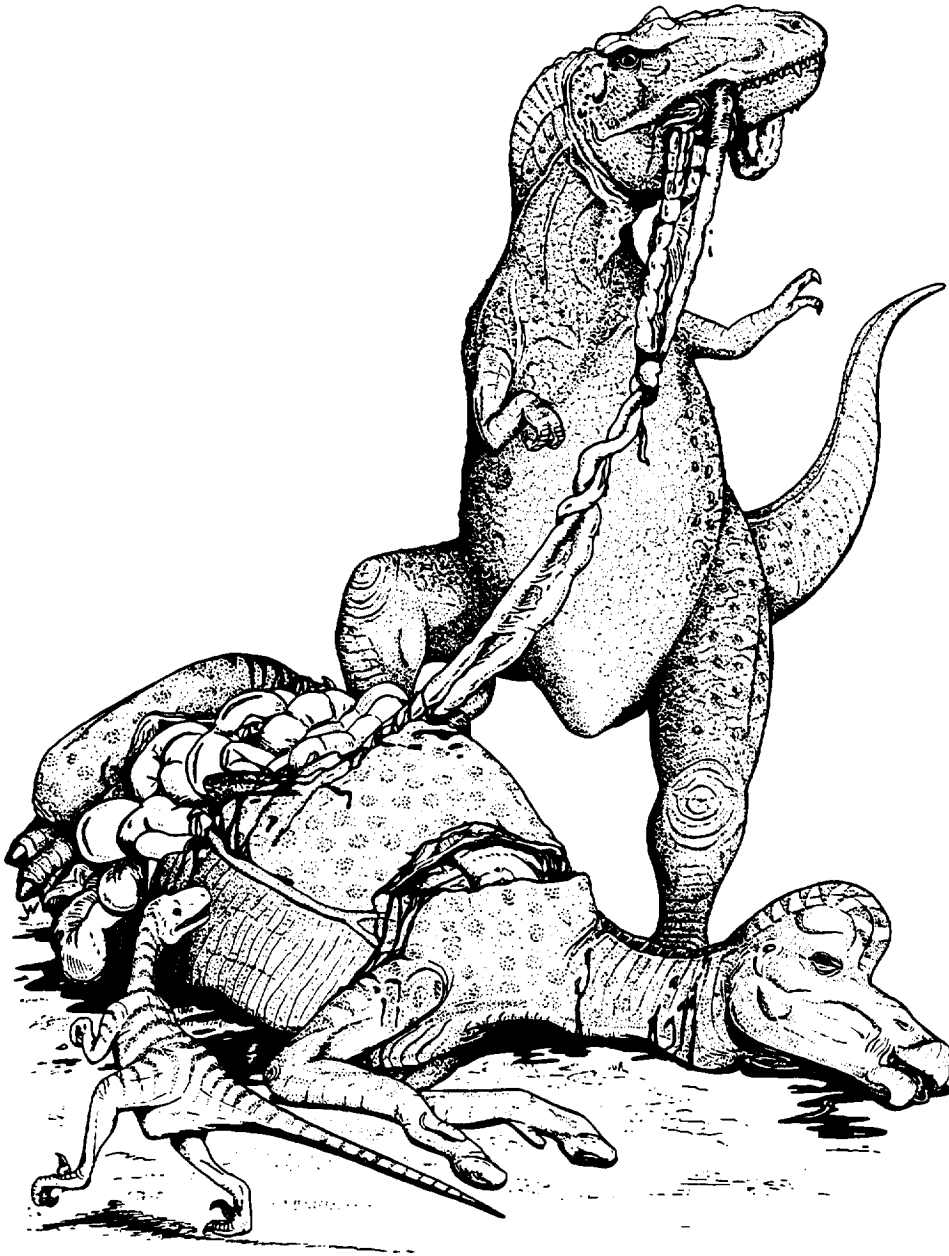

Figure 5--The Judith River tyrannosaurid *Albertosaurus* (as it is presently called) keeping a lunch date with the hadrosaur *Corythosaurus*. Drawing by Jim Whitcraft.

Lambe (1917) attributed wear surfaces on the sides of tyrannosaur lateral teeth (Figure 3) to inadvertent grinding of upper jaw teeth against lower jaw teeth during biting, such that large wear surfaces developed on the inner faces of upper jaw teeth, and on the outer faces of lower jaw teeth (Akersten [1985] offered a similar explanation for a large medial wear facet on a *Smilodon* saber). Lambe's hypothesis seems entirely reasonable, but in our experience large, nearly flat wear surfaces frequently occur on the inner faces of shed tyrannosaur teeth, but seldom, if ever, on outer tooth faces (small lateral wear surfaces are not uncommon, however). Furthermore, a tooth *in situ* in a tyrannosaur lower jaw in the collection of the Canadian Museum of Nature (specimen number 2779) has a large wear surface on its inner face (we have seen somewhat similar medial wear surfaces on lower jaw teeth of a Komodo dragon [Harvard Museum of Comparative Zoology specimen number 24907]). Unless there is some preservation bias against lower jaw teeth, the occurrence of large wear surfaces on tyrannosaur lateral teeth seems inconsistent with Lambe's hypothesis. However, we are unable to offer any other explanation for the large medial wear surfaces.

Although our observations on wear surfaces on the incisor-like anterior teeth of tyrannosaurs are less extensive than those on lateral teeth, we presume that wear on the tooth tips and the marginal keels of anterior teeth was due to the same kind of stresses that wore the keels of the lateral teeth. We suspect that flat wear surfaces on the front and rear faces of these anterior teeth were caused by abrasion against prey victims' body, particularly their bones. However, more thorough study of wear surfaces of tyrannosaur anterior, incisor-like teeth is needed.

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Terramegathermy in the Time of the Titans: Restoring the Metabolics of Colossal Dinosaurs

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INTRODUCTION

Among dinosaurs, megadinosaurs (those over one tonne) have been considered among the best candidates for having had low metabolic rates (LoMRs). Spotila et al (1991) argued that big dinosaurs were gigantotherms that shared thermal characteristics with the large leatherback sea turtle, and Dodson (1991) suggested that giant dinosaurs lived in the slow lane compared to giant mammals. Coulson (1979), Bennett (1991) and Ruben (1991) restored big dinosaurs as "good reptiles" powered by bursts of reptilian hyperanaerobiosis rather than the sustained tachyaerobiosis that powers birds and mammals. Farlow (1990) suggested that large dinosaurs were "damned good reptiles" with fluctuating metabolic rates (MRs), and in 1993 he argued that dinosaurs used a combination of rapid reproduction and intermediate metabolic rates (InMRs) to grow bigger than land mammals. All the above workers, and McNab (1983) and Dunham et al. (1989), have modeled big dinosaurs as LoMR or InMR inertial homeotherms that maintained constant body temperatures on a daily basis.

Why land giants must be tachyaerobic. - We will outline arguments that megadinosaurs had high metabolic rates (HiMRs) similar to those of megamammals, except for a few InMR forms in both groups. Our hypothesis starts with a simple observation. On land all classic reptiles with LoMRs have weighed about one tonne or less (Figs. 1 & 2). Many HiMR land mammals have exceeded one tonne, and the largest approached 20 tonnes (Figs. 1 & 2). This differs from the marine realm, where 6-15 tonne basking and whale sharks have LoMRs, environmentally dependent body temperatures, and are more sluggish than the much more energetic and hotter running whales of the same size. Therefore, when we are asked (again and again) why some dinosaurs were four to five times bigger than land mammals, we ask why dinosaurs grew a hundred times larger than land reptiles!

Our hypothesis centers around the logical argument that living in the high energy field produced by gravity is a hard and constant struggle that can only be won with the great strength and sustained power inherent to a high energy tachyaerobic system. The belief that low energy bradyaerobic forms can bear the burden of great bulk is naive. Being an aquatic giant is much easier because water is a low energy environment where buoyancy negates the effects of gravity, and swimming is five to twelve times more efficient than walking the same distance.

Avian-mammalian versus reptilian chauvinism and other matters. - Some accuse those who have restored dinosaurs with HiMRs of being biased in favor of bird- and mammal-like metabolic
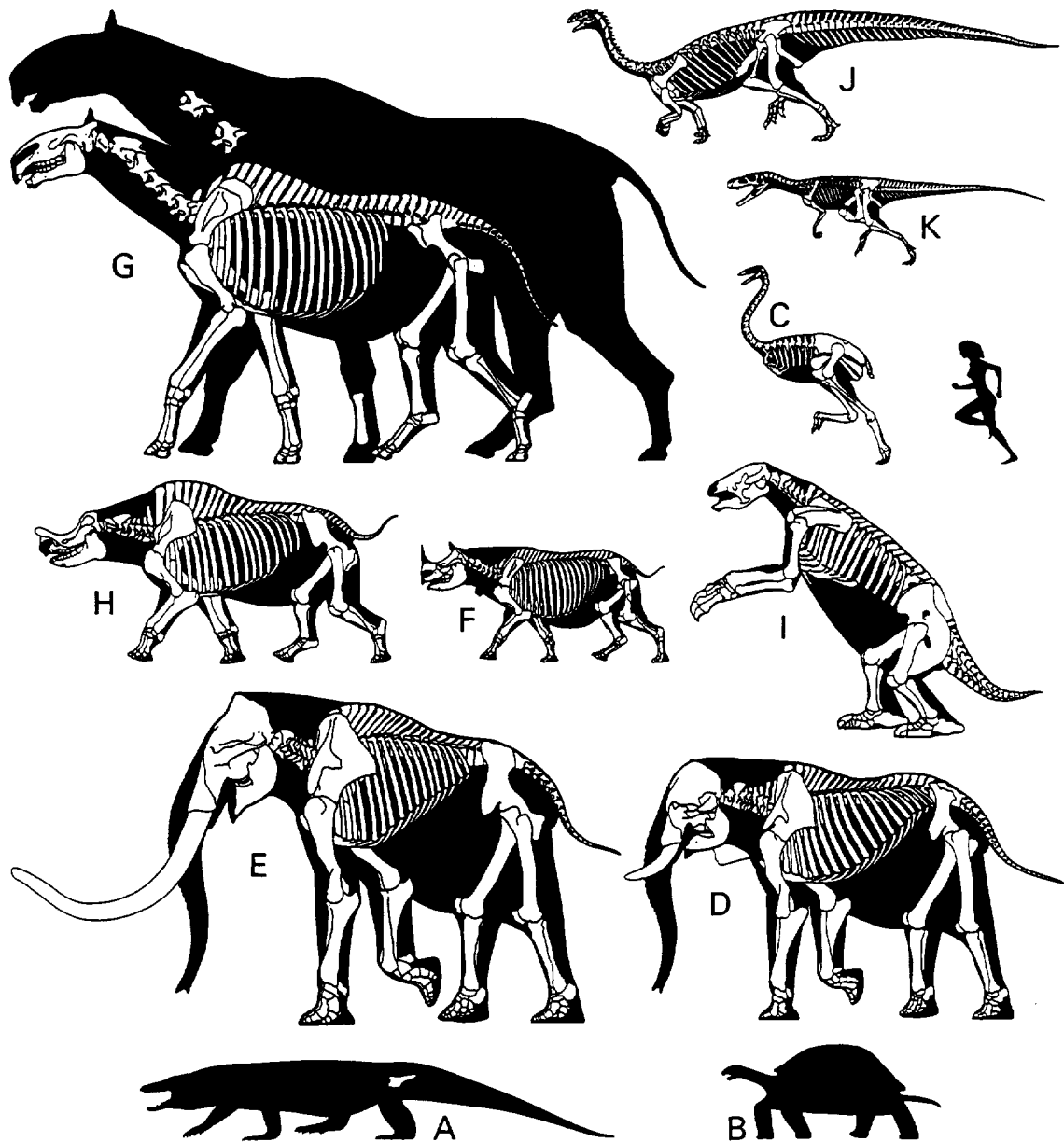
FIGURE 1 - Same scale figures of large land animals. A-B, largest extinct reptiles (0.8-1.0 tonnes), A, monitor Megalania (with preserved ilium), B, tortoise Geochelone atlas. C, elephant bird Aepyornis (0.4 t). D-H, megamammals, D, Loxodonta (6 t), E, Mammuthus (8 t), F, Rhinoceros (1.5 t), G, rhino Indricotherium (f 8 t, m 16 t), H, brontothere Brontops (3 t), I, sloth Eremotherium (4 t). J-K, brevischian dinosaurs, J, Herrerasaurus (0.2 t), K, Plateosaurus (0.8 t). L-T, megadinosaurs, theropods L, Allosaurus (1.3 t) and M, Tyrannosaurus (6 t), N, Therizinosaurus (6 t) and Nanshiungosaurus (1.2 t), sauropods O, Shunosaurus (3 t), and P, Camarasaurus (14 t), Q, Stegosaurus (2.2 t), R, ankylosaur Euoplocephalus (2.3 t), S, ceratopsid Pentaceratops (2.5 t), T, hadrosaur Shantungosaurus (10 t). Masses from volumetric models based on skeletal restorations.

4 m
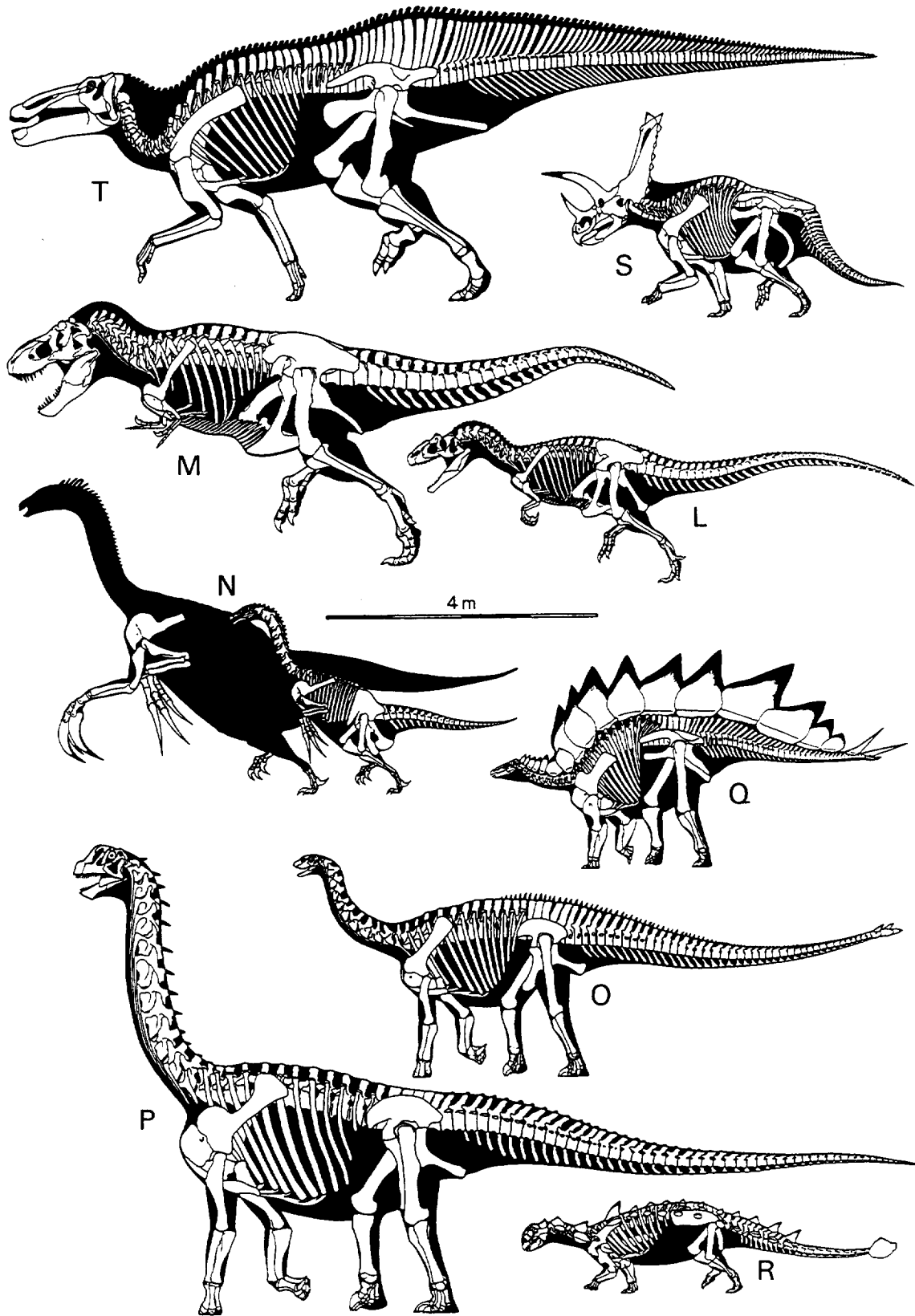
systems. However, an equivalent charge can be leveled at some of those who favor some form of reptilian or "intermediate" energetics for dinosaurs. We have no inherent preference for any metabolic system over another, and are interested only in which system best explains the phenomenon of dinosaurian gigantism.

In order to objectively diagnose the metabolics of megadinosaurs, this study follows some logical and conservative premises. Restorations of dinosaur metabolics should not be driven by theoretical ideas - such as the supposed superiority of reptilian or avian-mammalian systems, or that dinosaurian metabolics should have followed an exponential growth curve. Instead, the anatomy and biology of dinosaurs must be used to restore their metabolics before the evolution of their energetics can be understood. In order to minimize speculation we prefer to fit dinosaurs with anatomico-metabolic systems that are known to work in living forms over theoretical models unless the latter are unavoidable. In choosing living analogs for megadinosaurs we prefer forms that are closest to them in form and habitat - so large terrestrial creatures living under natural conditions are considered better analogs than aquatic, legless forms, or those raised under artificial conditions.

Leatherbacks versus elephants as dinosaur analogs. - Are sea turtles or land giants better living analogs for dinosaurs? Leatherbacks are legless forms with low capacity and low pressure respiro-circulatory systems. They live in a low energy world where cruising at high speeds and migrating long distances costs six times less energy than walking the same distance. Heat generated by internally placed muscles during constant swimming and trapped by heavy fat insulation helps maintain moderate body core temperatures of ~30°C. Leatherbacks never experience severe heat or tissue freezing temperatures.
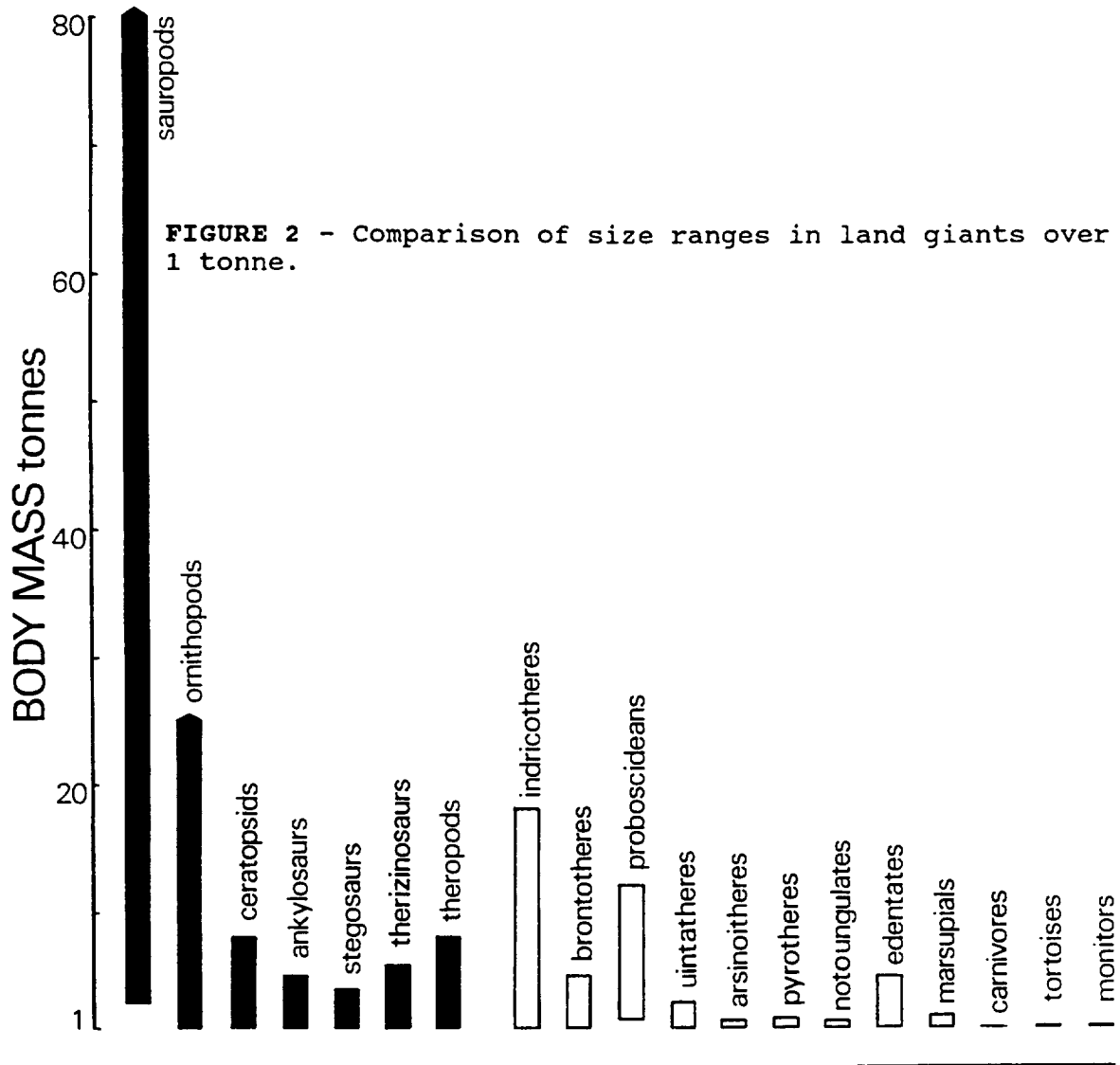
Elephants of the desert Skeleton Coast of southwest Africa have long striding limbs powered by large volumes of tachyaerobic muscles, high blood pressures, and high capacity respiratory tracts. These land giants do not cruise constantly, the leg muscles are placed away from the body core, and insulatory fat is absent (Haynes, 1991). Body core heat is generated largely by hard working internal organs. The Skeleton Coast elephants not only survive in a desert with limited resources by expending large amounts of energy as they wander long distances in search of food (Bartlett & Bartlett, 1992), they are unusually gigantic with world record weights up to 10 tonnes. Rather than going belly up when it gets hot, they use high body temperatures of 37°C and bulk to thermoregulate in extreme heat. Proboscideans have experienced frostbiting temperatures (Haynes, 1991).

The form and habitat of leatherbacks could hardly be more different from the dinosaur world. Acceptance of their use as primary models for dinosaurs is therefore surprising - imagine the reaction if whales were used as the primary analogs for dinosaurs! The structure and hot climates of elephants are very reminiscent of the dinosaur condition, and it is surprising how many reject their biology when restoring dinosaur thermodynamics.

80

sauropods

FIGURE 2 - Comparison of size ranges in land giants over 1 tonne.

60

BODY MASS tonnes

ornithopods

40

20

indricotheres

proboscideans

ceratopsids

ankylosaurs

stegosaurs

therizinosaurs

theropods

brontotheres

uintatheres

arsinoitheres

pyrotheres

notoungulates

edentates

marsupials

carnivores

tortoises

monitors

1

METABOLIC CHARACTERISTICS OF LIVING GIANTS

Muscles, blood pressures and breathing. - The great strength and endurance needed to carry great bulk are provided by large muscles. The skeletal muscles of birds and mammals are about twice as large as those of reptiles at a given body size (Ruben, 1991). Reptiles, including the largest, have correspondingly small legs, with narrow thigh muscles that are anchored upon correspondingly small ilia (the upper pelvic bone, Fig. 1A). The large legs of birds and mammals, including slow gigantic elephants, have broad thigh muscles supported by large ilial plates (Fig. 1C-I). A plot comparing ilium length in land animals confirms that birds and mammals have much bigger pelvic bones than reptiles (Fig. 3; a comparison of ilium surface area is preferable but was not feasible). Are large ilial plates required to support great mass, for erect legs, or for bipedal posture? The connection between the vertebral column and pelvis in bipedal and in big mammals is much shorter than the ilium. Bipedal birds
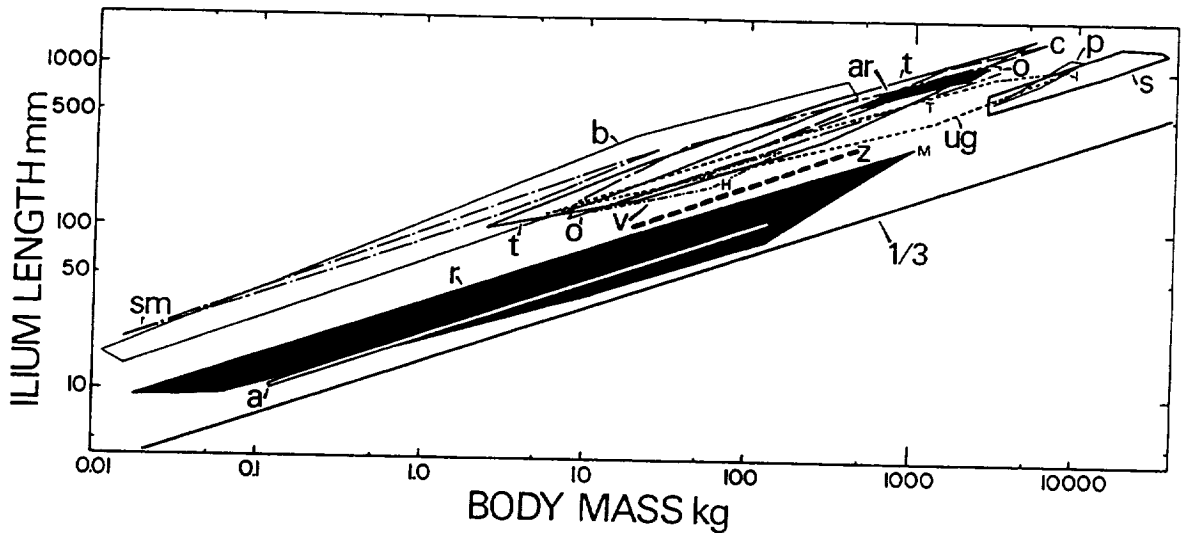
FIGURE 3 - Length of the ilium - the upper pelvic bone that anchors the thigh muscles - in land animals: r, reptiles; M, _Megalania_; a, alligator growth curve (courtesy P. Dodson); b, birds; sm; saltorial mammals; H, human; v, carnivores; ug, ungulates; I, indricothere; p, proboscideans; z, brevischian staurikosaur, herrerasaur, prosauropod; t, theropods; T, therizinosaur; s, sauropods; ar - stegosaurs and ankylosaurs; c - ceratopsids; o - ornithopods.

and saltorial mammals have longer ilia than quadrupedal mammals, but the ilia of the latter are much longer than in reptiles. Some bipedal, erect-limbed dinosaurs had short ilia. The sole purpose of large ilia is to support large leg muscles.

Why do reptiles have such small leg muscles, and birds and mammals such large ones? One reason is that reptile muscles can produce twice as much anaerobic power as those of mammals and birds (Ruben, 1991), so even small legged lizards and crocodilians sprint at high speeds. However, hyperanaerobiosis is an inefficient process (that consumes ten times as much food as aerobiosis) that works for only a few minutes, and is followed by toxic effects (Bennett, 1991). For example, anaerobic power falls off so quickly that big crocs may be unable to drag smaller ungulates into deep water to drown them if they do not succeed with the first lunge (Deeble & Stone, 1993; contrary to the assertion of Bennett et al. (1985) that big reptiles can produce hyperanaerobic power for long periods). A croc or gator can outsprint a person, but loses speed after a few seconds (Grenard, 1991). Also, large reptiles are at high risk of death after long periods of intense exercise because large animals cannot quickly recover from the toxic effects of anaerobiosis (Bennett et al., 1985). The lower anaerobic power production of tachyaerobic muscles means that birds and mammals need larger leg muscles than reptiles to produce as much overall burst power. The inability to carry massive bulk with small anaerobic muscles helps explain why really gigantic reptiles have always been aquatic.

In addition to anaerobic factors, the aerobic capacity of the respiro-circulatory system determines the size of the leg musculature. The low capacity and low pressure respiro-circulatory system of reptiles can deliver only enough oxygen to supply small bradyaerobic muscles. The large, tachyaerobic muscles of exercising birds and mammals demand large amounts of oxygen. The only way the muscles can get so much oxygen delivered to them is via large volumes of blood that are driven by high circulatory pressures, and oxygenated by a high capacity respiratory system. The ability of mammals to oxygenate large sets of leg muscles helps explain why some became land giants.

There is another reason why giants need high blood pressures. Pumping blood up against the gravity well to the brain requires work. The higher the blood is pumped the harder the work must be - and following the adage that one cannot get something for nothing, we presume this is true even if special cardiovascular adaptations are present. It is not possible to pump blood more

FIGURE 4 - Same scale figures of a 30 tonne Brachiosaurus and a 30 tonne female sperm whale. The dinosaur is restored with an 11 m long trachea, lungs and a super high pressure 1 tonne heart. The whale's 7 m long anterior airway, small lungs and normal high pressure 150 kg heart are shown.

184
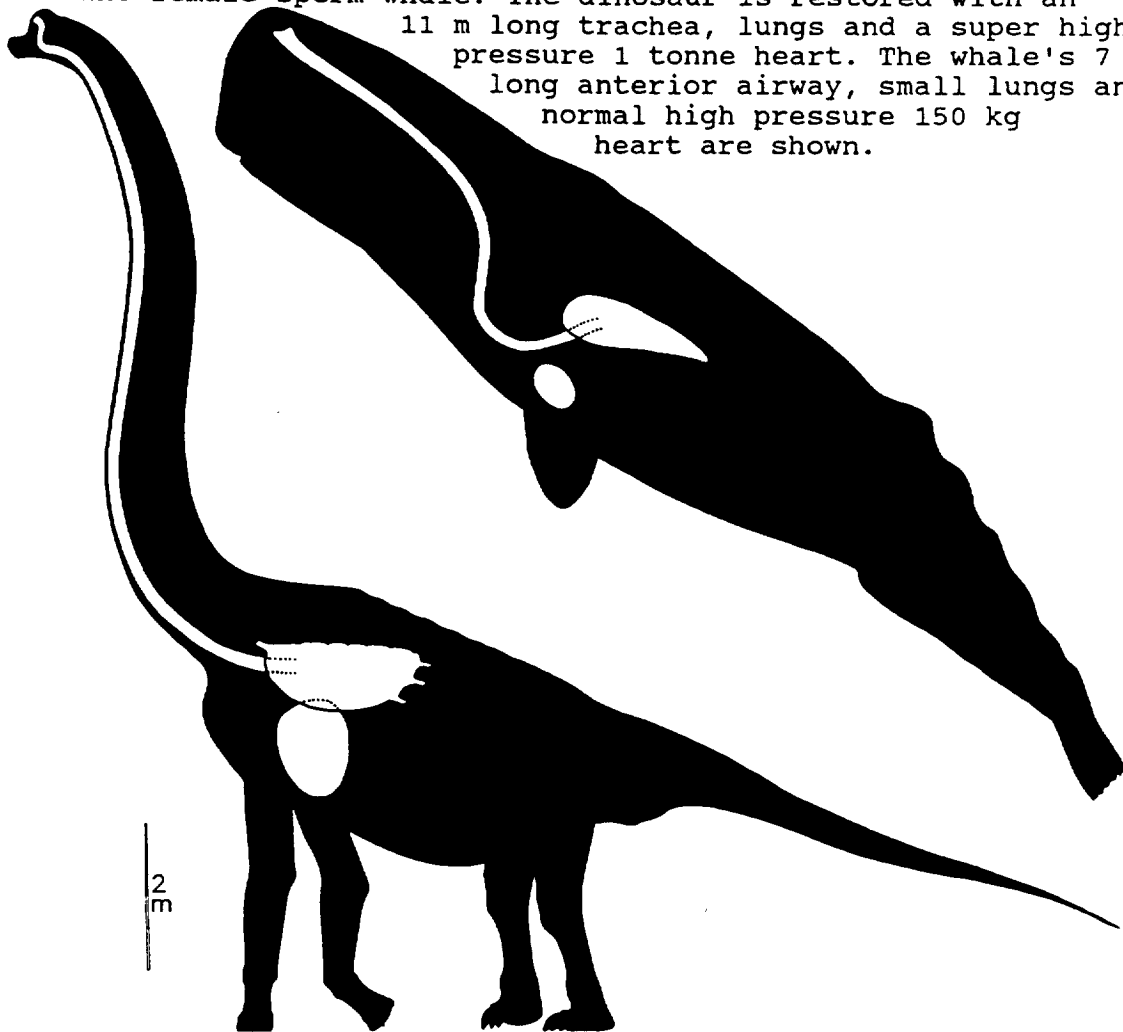
than 0.5 m above heart level with low, reptilian circulatory pressures and bradycardiac work (Seymour, 1976), so no land reptile has a long erect neck. The high pressure hearts of most mammals, from mice to humans, elephants, and whales, make up about 0.6% of body mass (Fig. 4, Table 1). Long necked giraffes have oversized hearts that produce unusually high pressures (Table 1).

A consequence of high aerobic capacity and high circulatory pressures is high resting MRs. In order to process large volumes of oxygen when exercising, tachyaerobic muscle cells have "leaky" membranes that require that the cell consume large amounts of oxygen in order to resist osmotic flow and maintain a proper chemical balance with surrounding tissues (Else & Hulbert, 1987). Failure to properly oxygenate the tissues of tachyaerobic animals results in a shutdown of the system causing torpor, so failure to maintain high blood pressure even when resting results in torpor.

Maintaining high resting blood pressure requires that the heart work hard. The respiratory system must also work hard to supply the hard working heart and other tissues with large volumes of oxygen. The liver and kidneys must work hard to process the wastes produced by the hard working respiro-circulatory system. To supply the hard working organs with large volumes of food the digestive tract must work hard. The high oxygen consumption of tachyaerobic cells and the hard working internal organs adds up to a resting metabolic rate that is nearly as high as the entire oxygen consumption of active reptiles with low pressure circulatory systems (Jansky, 1965, who notes that cardiac work is an increasingly large part of the resting metabolism in larger mammals). This is why vertebrates always have low exercise/ resting aerobic ratios.

Long anterior airways pose a respiratory problem because they hinder ventilation of the lungs. Even so, sperm whales (Fig. 4) inhale enough air through long anterior airways to sustain HiMRs with modern oxygen levels. This is true despite the small size of their lungs, the lack of respiratory air-sacs, and the need to respire during brief periods at the surface between long dives.

Cruising and migration. - In order to forage long distances on a daily basis, or to migrate very long distances on a yearly basis, sustained walking speeds should be above 2-3 km/h. Because moving on land is energy expensive, high aerobic capacity is needed to power such high cruising speeds for many hours (Bennett, 1991). This is true of large as well as small animals. The 2-7 km/h walking speeds observed in elephants for example (Fig. 5) are easily achieved aerobically. Although swimming leatherbacks cruise at 3-5 km/h, the sustainable aerobic capacity of leatherbacks can power walking speeds of only 0.5-0.8 km/h (Fig. 5). The long migrations of leatherbacks are possible only because they swim so cheaply, and exploit favorable currents - land does not convey animals in this manner. Anaerobiosis does not produce power long and efficiently enough to power high walking speeds, so calculations that bradyaerobes can migrate farther than tachyaerobes on land (Spotila et al. 1991) are incorrect, and no land reptile migrates.

20
elephants 379

3
rhinos 45

3
42
tridactyl dinosaurs

8
ceratopsid
nodosaur
sauropods
62

0 1 2 3 4 5 6 7 8 9 10

km/h
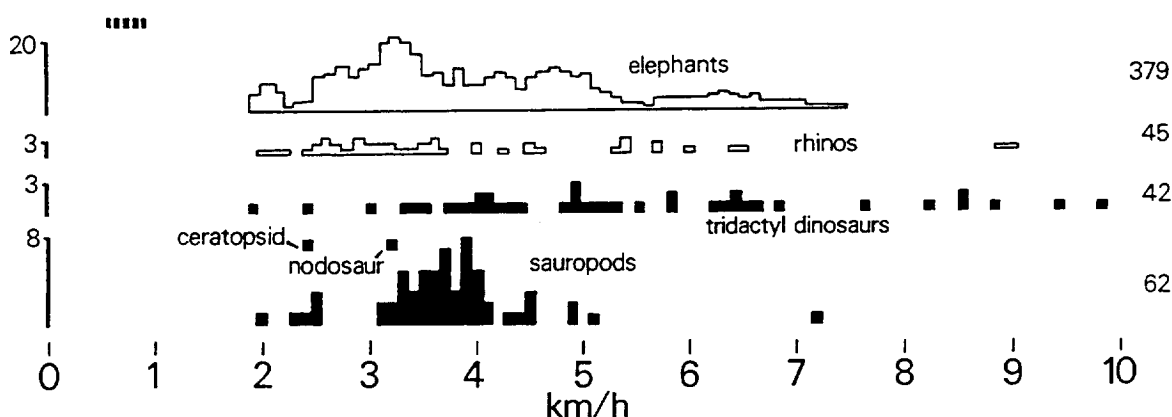
FIGURE 5 - High cruising speeds in megamammals and megadinosaurs over 1 tonne. Elephant and rhino speeds from videos, ornithopod, theropod, ceratopsid, ankylosaur and sauropod speeds estimated from trackways (incl. Currie, 1983; Lockley et al., 1986; sauropod data courtesy J. Farlow). Upper left bar indicates the low sustained walking speeds predicted by the reptilian aerobic metabolism of a cruising leatherback sea turtle.

Galloping rhinos do not have higher resting MRs than slower elephants, although their exercise MRs may be higher. The most gigantic extinct mammals were 10 to 20 tonne, HiMR proboscideans and indricotheres with long striding legs (Fig. 1D,E,G). Giant extinct edentates and marsupials with heavy awkward limbs never exceeded about 5 tonnes (Fig. 1I), and these rather sluggish beasts probably had InMRs like their living relatives (McNab, 1983). If so, land animals much over 5 tonnes may need HiMRs.

Heterometaboly. - Farlow (1990) suggested that nonmammalian giants may be able to save energy by sharply dropping their MRs from high to low levels on a seasonal basis, or when they complete growth. Birds and mammals can drop mass specific MRs by about a third under similar circumstances. Greater metabolic declines are probably not feasible in vertebrates because suppressing MRs strongly decreases cardiac work and circulatory pressures, resulting in impaired aerobic capacity and torpor.

Growth and reproduction. - Fig. 6 shows that land reptiles grow more slowly than birds and all but a few terrestrial HiMR mammals (Case, 1978). Note that the divergence between terrestrial reptilian and mammalian growth rates increases with size; this negates the premise of gigantothermy that the growth rates of land giants should converge towards a common level. The inability of bradyaerobic juveniles with low foraging speeds and ranges to gather enough food is one reason they grow slowly. It has been suggested that elevated growth rates of farm-raised alligators and captive leatherbacks show that reptiles can grow rapidly. Raising alligators is an energy expensive and labor intensive proposition that involves providing idle reptiles with large quantities of food (Grenard, 1991). The relevance of captive and or aquatic reptilian juveniles to natural land conditions is nil.
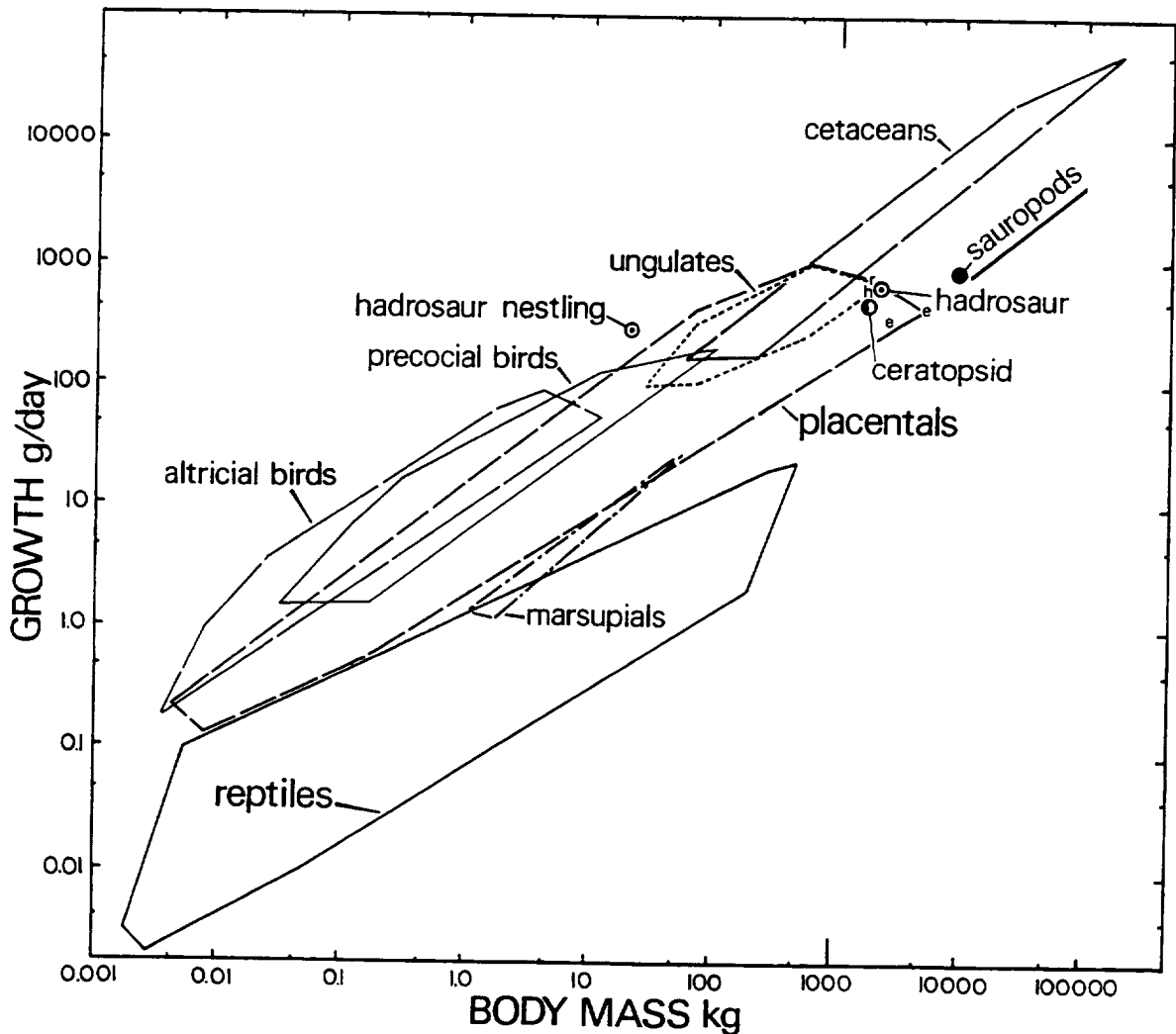
FIGURE 6 - Growth rates in land tetrapods and whales, r, white rhino, h, hippo, e, African elephants. Data for modern animals in part from Case (1978). Growth rates for megadinosaurs based on nesting periods and size distribution patterns in bonebeds (Currie & Dodson, 1984; Horner & Gorman, 1988) and bone rings (Reid, 1990). Minimum growth rates needed for giant sauropods to reach sexual maturity at 1/3 adult mass is indicated.

In order to maintain stable populations over time, generational turnover must be sufficiently rapid. Giants must therefore reach sexual maturity within about twenty years and their lifespans should not be much greater than a century (Dunham et al., 1989). Big ungulates, rhinos, elephants, and whales fit these characteristics (Owen-Smith, 1988). Note that the more gigantic an animal is, the higher the rate of growth must be in order to keep the juvenile stage and lifespan within reasonable limits. We conclude that HiMRs are necessary to grow more than 5 tonnes. The large size of some extinct marsupials and edentates suggests that InMRs are sufficient to grow to about 5 tonnes, and LoMRs can grow animals to only about 1 tonne.
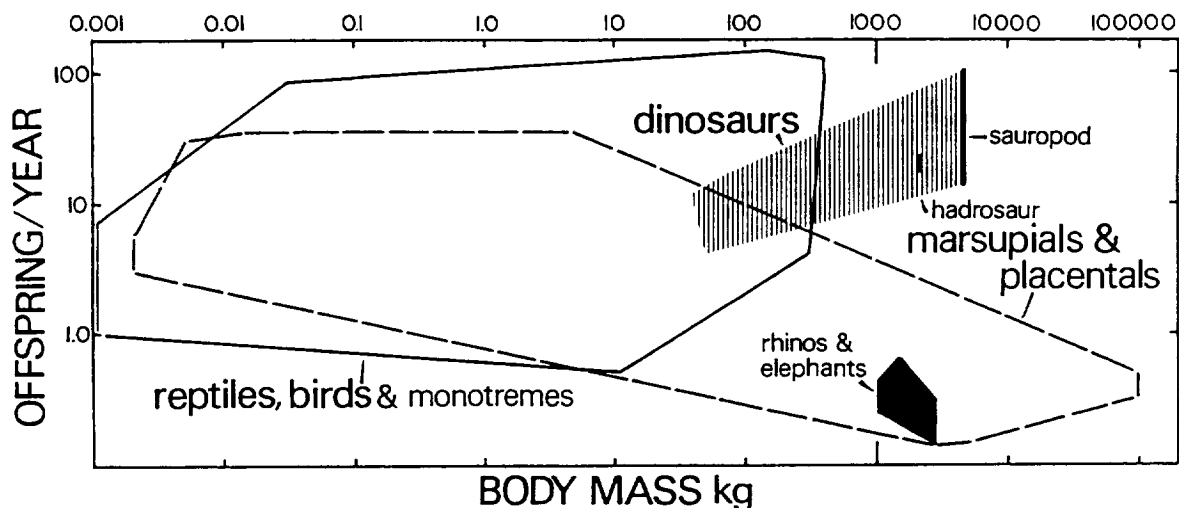
FIGURE 7 - Rates of reproduction in egg laying and live bearing tetrapods compared to dinosaurs, values for two megadinosaurs indicated with solid bars. For more details see Paul (1994).

A problem with being a tachyaerobic giant is that each adult consumes large amounts of food, so the total adult population size is rather small (Farlow, 1993; Paul, 1994). Small HiMR mammals and birds and LoMR reptiles can have much larger adult populations than megamammals. In general, small populations are less stable than larger ones over geological time. Big mammals produce a few (Fig. 7) fast growing calves that are highly dependent upon their parents for survival. Under optimal natural conditions megamammals can expand their populations about 6-12% per annum (Owen-Smith, 1988). These modest rates of population expansion have allowed megamammals to evolve moderately gigantic masses during the Cenozoic. Large reptiles lay large numbers of eggs, but their slow growth and generational turnover hinders their ability to exploit their rapid reproduction to evolve giant dimensions. We predict that if giants combine high rates of growth with high rates of reproduction, then the resulting high rates of population expansion - perhaps over 100% under optimal conditions even with high juvenile mortality - should allow them to survive as species even if the adult populations are so small that they are prone to periodic crashes. If so, then fast breeding tachyaerobic giants have the potential to have smaller populations of larger adults living off of the same resource base than observed among slow breeding big mammals (Paul, 1994).

Socialization and parenting. - The most parental of reptiles are semi-aquatic crocodilians that move only short distances around their nests and expend little energy as they swim after their charges in water. Crocodilians do not forage for their young, and they care for them only while they are very little. Terrestrial reptiles do not have the energy to care for their young, or to engage in the extended social activities associated with living in packs or herds. Extended parental care, foraging for the young, and organized groups are observed on land only in tachyaerobic birds and mammals.
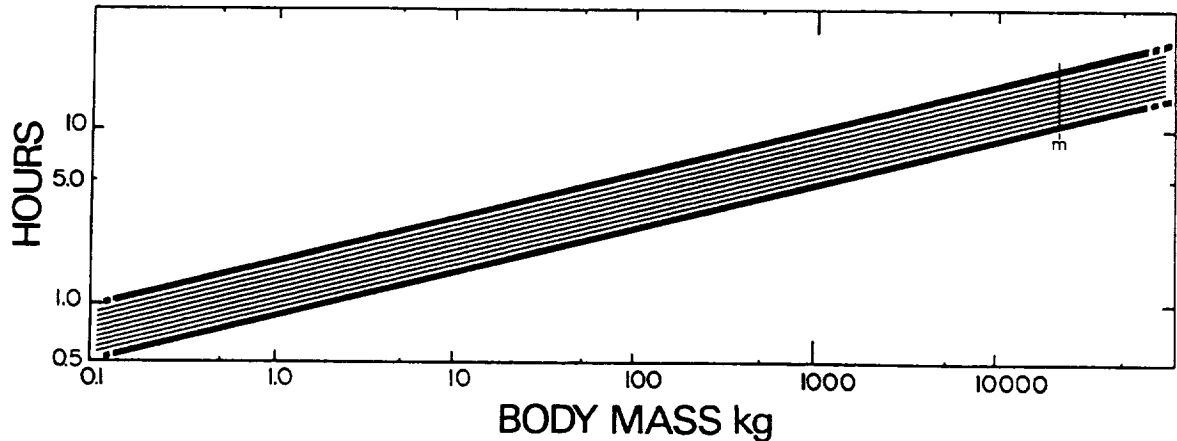
FIGURE 8 - This plot shows the time it takes for HiMR animals to overheat if they store all internally generated heat and exclude external heat with high body temperatures increasing to 46°C. The size of the largest mammals is indicated. For details of the calculations see Paul (1991).

The big overheating myth. - It is a nearly universal truism that giant HiMR endotherms are in danger of "frying" or "melting down" in hot climates. Spotila et al. (1991) calculate that an inactive 3.6 tonne tachyaerobe will have a body temperature of 53°C when the environmental temperature is 35°C. The reality is that desert elephants traverse shadeless land in the middle of hot days, and even when chased by helicopters elephants do not heat up to dangerous levels (Bartlett & Bartlett, 1992 and Osborn, 1992, pers comms.). In hot droughts the big bulls suffer the lowest mortality, and females and calves die largely from starvation (Owen-Smith, 1988; Haynes, 1993), there are no documented examples of elephants dying from heat stroke under natural conditions. Extinct elephants, mammoths and indricotheres of 10 to 20 tonnes thermoregulated in hot climates.

Giant tachyaerobes have relatively low MRs per unit body mass, enormous heat storage capacity, and high body temperatures of 36-39°C. A basic thermodynamic principle is that machines that operate in hot environments should be built to run at hot temperatures. An active tachyaerobe of 4 tonnes with a normal body temperature of 39°C can resist the inflow of an external heat load well over 40°C by raising its body temperature to 43-46°C. Internal heat is safely stored for about six hours (Fig. 8), and is later dumped into the night sky.

What it takes to be gigantic in 1 G. - The common idea that LoMRs are ideal for land giants fail in the absence of any living examples, and the success of HiMR megamammals. The inability of land reptiles to grow rapidly on land under natural conditions may be a critical failure that prevents them from being gigantic. If they did manage to grow much over a tonne, low circulatory pressures and small limb muscles would prevent them from functioning. The temperature stability of LoMR inertial homeothermy does not provide giants with the power they need to

be so big. It is water giants that have no need for high blood pressures or large volumes of hard working limb muscles.

Owen-Smith (1988) described how land dwelling megamammals have thrived in the Cenozoic because of their rapid growth and good population recovery, ability to cope with climatic extremes, their powerful and nonselective feeding adaptations, slow rates of starvation, and their ability to wander far in search of the best conditions. This is the high energy system based on high aerobic power needed to be gigantic. Large tachyaerobic muscles support great bulk for long periods, and to move the bulk fast and far enough to find food during long droughts. Because land giants must have large tachyaerobic muscles, and often must pump blood far up to their brains, they are forced to have high circulatory pressures. The consequences of high blood pressures are high aerobic scopes and high resting metabolisms. The rapid growth sustained by HiMRs is necessary in order to reach adult size in a reasonable time. We predict that fast reproduction allows tachyaerobes to grow larger than terrestrial megamammals.

THE METABOLICS OF MEGADINOSAURS

Big sauropods (such as brachiosaurs, supersaurs and titanosaurs like new Argentinosaurus) reached 40 to 100 tonnes (Fig. 2). Skeletons and enormous footprints indicate that some bipedal ornithopods weighed as much as 10 to 30 tonnes (Fig. 1T). Predaceous theropods exceeded 5 tonnes. Bigger dinosaurs wait to be discovered, and rare "world record" individuals will never be found, so 100+ tonners are likely to have existed!

Hips, legs and cruising. - Early dinosaurs - eoraptors, staurikosaurs, herrerasaurs and prosauropods - had erect legs like birds and mammals, yet they retained short, reptile-like ilia (Figs. 1J,K & 3). These ilia could have only supported narrow thigh muscles like those of reptiles. The combination of erect limbs and reptile-like hips was an unusual and exotic combination that is now extinct. It suggests that these early "brevischian" dinosaurs had aerobic metabolics that were neither reptilian or avian-mammalian in nature, and that MRs, circulatory pressures, cruising speeds and growth rates were insufficient to achieve great size - so it is not surprising that no small-hipped dinosaur became very big. These archaic dinosaurs may fit the definition of "damned good reptiles".

The early dinosaur condition was not a very satisfactory one because the full potential of the long erect legs could not be realized until the size of the ilium and the leg musculature expanded to avian-mammalian proportions. This is the condition observed in "longoschian" theropods, therizinosaurs, ornithischians and sauropods of all sizes (Figs. 1L-T & 3). Among megadinosaurs, the ilial plates of tyrannosaurs are so large that a high endurance limb musculature suitable for chasing down large prey is indicated over ambush or scavenging habits. The prey of tyrannosaurs - hadrosaurs and especially the ceratopsids - also had long ilia that appear to have supported large sets of aerobically capable muscles suitable for running. Slower moving

armored dinosaurs and sauropods are restored with large tachyaerobic limb muscles suitable for bearing great bulk. There is nothing reptilian about the hips and legs of longoschian megadinosaurs; instead, their form is bird- or mammal-like. The suggestion that the muscles of large dinosaurs were small and hyperanaerobic is therefore contra-indicated.

Most megadinosaurs had long striding limbs like those of fast cruising ungulates and elephants. Figure 5 shows that the estimated speeds of bipedal and quadrupedal dinosaurs are similar to those of elephants, and are much higher than those predicted in big reptiles. This proves that megadinosaurs walked in the same fast lane as HiMR megamammals, not in the reptilian slow lane. Only the bizarre advanced therizinosaurs (Fig. 1N) had awkward feet suggestive of InMRs like those of giant sloths. It is widely agreed that some megadinosaurs migrated long distances (Currie & Dodson, 1984; Horner & Gorman, 1988); such journeys demanded high aerobic capacity.

Circulatory pressures. - It has been widely accepted that big theropods had strongly S-curved necks that carried the brain well above heart level, and the same was true of the therizinosaurs (Fig. 1L-N). There has been much more controversy over the neck posture of sauropod dinosaurs. It has been argued that the long necks of sauropods evolved for high browsing and must have been held erect, or that circulatory pressure problems compelled them to carry their necks horizontally (Dodson, 1991), but no one has examined the articulation of sauropod necks in order to restore their true posture. Articulated specimens of Camarasaurus and Chinese sauropods consistently show an upward flexion at the base of the neck (Figs. 1,O,P & 9). The tall shoulders present in many sauropods (a cetiosaur, brachiosaurs, camarasaurs, omeisaurs, mamenchisaurs, euhelopids, many titanosaurs) favored an erect

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TABLE 1

Heart size and heat production in a 30 tonne Brachiosaurus

Resting MR in kcal/hour if it is.....
mammalian....................................**4000-8000**
reptilian.......................................**500-900**

total heart tissue mass as % of total body mass	in kg	cardiac heat production kcal/hour
0.6% single normal (BP 100-130 mmHg)	180	1000
1.3% single giraffe oversized (BP 200 mmHg)	400	
2.0% multiple cervical (BP 200 mmHg)	700	¯2000
3.3% single super oversized (BP 750 mmHg)	1000	¯3000
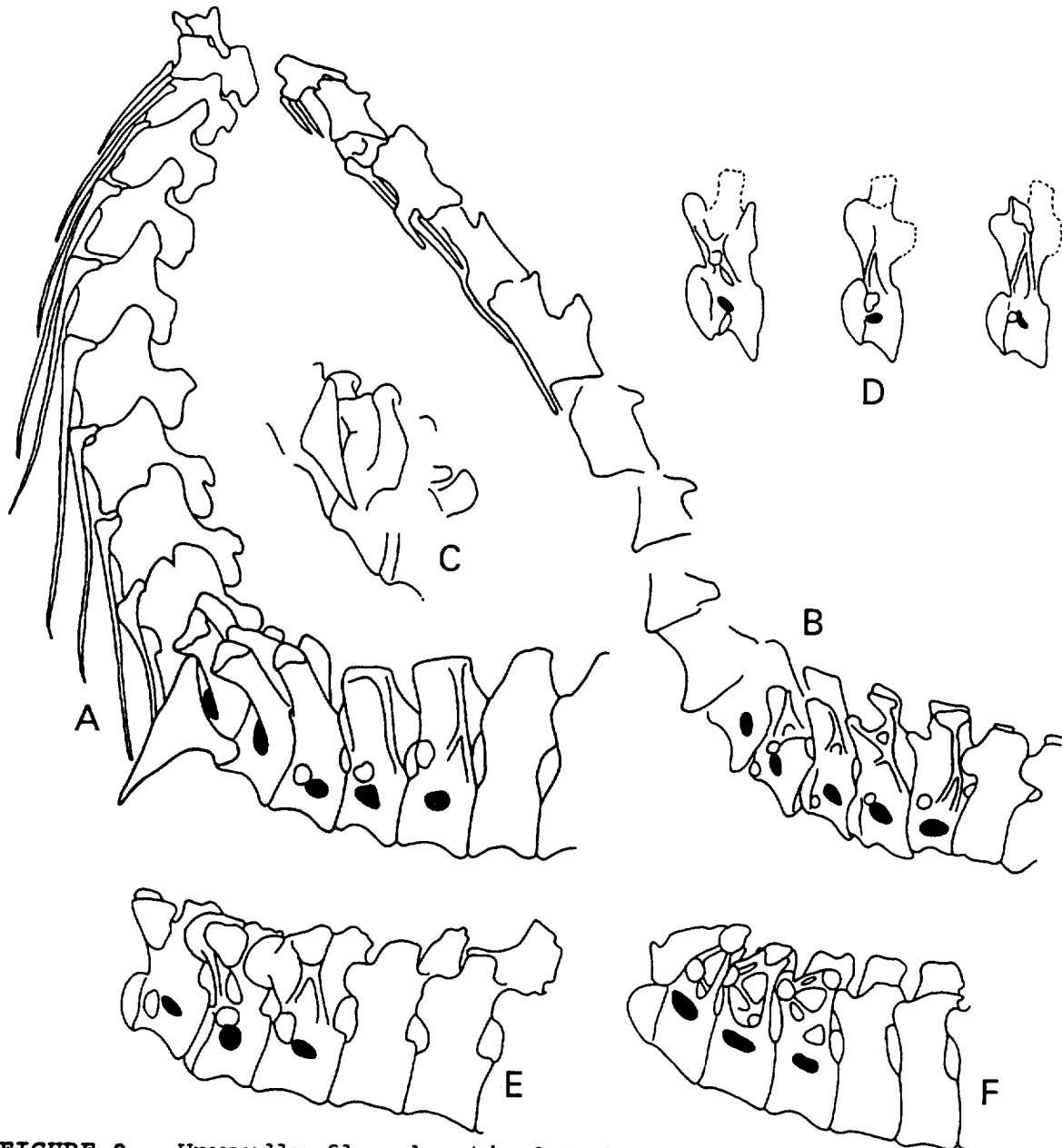
FIGURE 9 - Upwardly flexed articulated neck bases and beveled cervo-dorsals indicating habitually erect neck carriage in the sauropods A-D, _Camarasaurus_ and E-F, _Euhelopus_.

neck posture. Low shouldered diplodocids had horizontal necks, but large sacral complexes and heavy tails suggest they reared up to feed. Retroverted hips suggest that camarasaurs (Fig. 1P), mamenchisaurs and euhelopids also reared up often.

One way or another, sauropods had to pump blood all the way up their necks. Consider the problem faced by a 30 tonne _Brachiosaurus_ (Fig. 4). We conservatively presume that even with special vascular adaptations a low power reptilian heart could not pump blood up 10 m. Even if the sauropod had a normal sized

high pressure heart of 180 kg, the metabolic rate of the heart alone would be greater than that of the entire resting metabolism of a giant reptile (Table 1). If the heart had giraffe-like proportions it would have weighed 400 kg, but even this would not suffice to pump blood up over 30 ft. Seymour (1976) calculated that Brachiosaurus needed a supersized heart of over a tonne, and a one tonne heart is the largest that could fit into the sauropod's ribcage. Such a heart would be inefficient, and Choy & Altman (1992) made the interesting and controversial suggestion that sauropods had extra hearts in the neck so that the main heart would not need to be so huge. In either case, conservative calculations of cardiac heat production are many times higher than the resting metabolism of a reptile. When the heat production of the other internal organs is added in, it is clear that the resting MR of Brachiosaurus was as high as those of giant mammals, and many times higher than expected in a reptile of such size (Table 1).

It has been calculated that long necked sauropods could not draw enough air down their long trachea to sustain HiMRs (Daniels & Pratt, 1992). Alternately it has been calculated that elevated oxygen levels were necessary to sustain sauropods (Hengst, this volume). Although we take no particular position on Mesozoic oxygen levels, we strongly question whether the respiratory capacity of dinosaurs can be calculated accurately enough to estimate past oxygen levels. Nor do we predict that sauropods had any more trouble breathing large volumes of air with modern levels of oxygen than do sperm whales. The surface of sauropod trachea may have been aerodynamically configured to maximize airflow. Although sauropods probably lacked a mammalian diaphragm, thin walled, pneumatic vertebrae strongly suggest the presence of pulmonary air-sacs. Because sauropods were not close bird relatives, we predict that their air-sac/lung system operated in a different manner (note even some birds have sternal plates that are too small to ventilate abdominal air-sacs, Fig. 1C). Abdominal air-sacs operated by long posterior ribs probably improved pulmonary air exchange enough to oxygenate HiMRs.

Large theropods had pneumatic vertebrae that suggest a pre-avian air-sac system was being developed. Progressive elongation of posterior over anterior ribs suggest that ventilation of abdominal air-sacs became important in large theropods (Fig. 1L,M). Perry (1983) suggested that the prepubis and retroverted pubis/ischium of large ornithischians supported abdominal muscles that functioned like a diaphragm. Large ornithopods had a lumbar space that lacked long ribs, and was preceeded by long mid-dorsal ribs. This was a very mammal-like condition (compare Fig. 1D-H to 1T), and strongly suggests that ornithopods paralleled mammals in developing a vertical transverse diaphragm. Giant dinosaurs appear to have had high capacity respiratory systems designed to oxygenate their high capacity circulatory systems.

Growth and reproduction. - Estimated rates of growth for large duckbilled, horned, and ceratopsid dinosaurs suggest that giant dinosaurs grew as rapidly as rhinos and elephants of similar size (Fig. 6). MRs similar to those of big edentates, rhinos, elephants, and whales were necessary for big dinosaurs to grow up

within reasonable time spans. Reptilian or intermediate metabolics would not have done the job under natural conditions. As the tallest and most massive sauropods grew, their increasing height and the very rapid growth needed to mature in due time are especially interesting. Even InMRs were probably not adequate for such fast growth, and the increasing cardiac work associated with increasing height suggests that mass specific MRs increased with maturity rather than falling off somewhat in the normal manner.

Why did some dinosaurs become bigger than land mammals? - Modern restorations (including the senior author's) that show dinosaur parents caring for a small number of youngsters in the manner of big mammals are not accurate. The egg laying megadinosaurs out-reproduced megamammals by a factor of dozens to hundreds (Fig. 7). Also, non-nursing, post-nestling juvenile dinosaurs were not as dependent upon adults for survival as are mammalian young. Megadinosaurs fit the ideal of being fast growing, fast reproducing forms that could achieve long term survivability with small, unstable populations of enormous adults - a feat attainable only with HiMRs (Paul, 1994).

Parenting and social organization. - The modern consensus is that megadinosaur socialization was highly variable and often well developed (Currie, 1983; Lockley et al., 1986; Horner & Gorman, 1988). Many examples lived in herds or packs and cared for their young, in some cases by foraging for nestlings. This was above the crocodilian level of socialization, and approaches the avian-mammalian condition. Only tachyaerobic dinosaurs could have sustained such intense social activity on land.

Megadinosaurs did not meltdown. - Tachyaerobic dinosaurs up to 20 tonnes would have had no more trouble thermoregulating in hot climates than have tropical mammals of the same size. A 40 tonne tachyaerobic sauropod with a high body temperature would have been able to safely store internally generated heat for 12 hours (Fig. 8). We restore tropical megadinosaurs with 2-7% body fat (as in tropical ungulates and proboscideans, Ledger, 1968; Haynes, 1991), rather than heavy domestic animal-like fat deposits postulated for gigantothermic dinosaurs (Spotila et al., 1991). Polar megadinosaurs probably built up fat deposits for winter use; whether they used it for insulation is more problematic (see Haynes, 1991).

Could tachyaerobic sauropods feed themselves? - Astute observers of <u>Jurassic</u> <u>Park</u> noticed that the brachiosaur's head was big enough to swallow the kids whole. A 30 tonne HiMR brachiosaur needed to eat about half a tonne of fodder/day, only 1.5% of its own mass. If the beast took.six bites per minute for twelve hours per day (as per giraffes and elephants) each bite would be a mere four oz., hardly a problem for a mouth that was 42 cm broad. A 10 tonne HiMR diplodocid needed only 2 oz. bites.

Megadinosaurs were not weak. - Over the years it has been asserted that sauropods could not move on land, rear up, feed HiMRs, or pump blood up their long necks, that large dinosaurs had limited breathing capacity and moved slowly, and that big theropods were mere scavengers - it is amazing that the 1-100

tonne weaklings survived at all! Examining the structure of megadinosaurs reveals strong animals of high aerobic capacity and great athletic ability. Figure 1 shows that at any given size, megadinosaur skeletons (especially their vertebral columns) were more strongly built than those of megamammals.

SUMMARY AND CONCLUSIONS

Megadinosaurs grew two orders of magnitude larger than any LoMR land reptile. They also regularly exceeded the 5 tonne maximum of sluggish InMR mammals. Giant dinosaurs (except the awkward footed therizinosaurs) shared large hips and long striding legs with the biggest ungulates and proboscideans. These hindlimbs were probably operated by large volumes of muscles which required large amounts of oxygen during exercise and when at rest. High capacity respiratory systems were probably present to oxygenate the large volumes of blood pumped to oxygen-craving muscles and high held brains by high pressure circulatory systems. An unappreciated consequence of the modern consensus favoring high pressure double pump hearts in dinosaurs is that the hard working hearts and supporting organs produced high avian-mammalian levels of heat production. Failure to maintain high internal pressures and high resting MRs would have resulted in torpor. Because large amounts of heat were generated by the muscles and organs even at rest, megadinosaurs were HiMR endotherms (except that InMRs are possible in therizinosaurs). The giant dinosaurs' fast growth was possible only because the juveniles had fast running metabolisms, and dramatic fall offs in MRs with maturity are not only contraindicated but may have been reversed in tall sauropods.

We do not assert that the physiology of megadinosaurs was identical to that of megamammals. The evolution of megadinosaurs in a warm Mesozoic world may have left low latitude examples with less well developed thermoregulatory controls and auxiliary heat production than is present in birds and mammals - but these features may have been present in polar dinosaurs. Smaller dinosaurs may have been more prone to entering daily torpor than modern birds and mammals. This may help explain why dinosaurs were more prone to laying down bone growth rings as they matured than are birds and mammals (Reid, 1990; Varricchio, 1992; but deep set postcranial rings are also observed in mammal bones [Leahy, 1991; Varricchio, [1992]). But, contrary to the argument that many dinosaurs had some form of transitional metabolics, the anatomical evidence shows that this condition was limited to early brevischian dinosaurs with their unusual combination of reptilian and avian features. There was little or nothing reptilian in the energetics of big bodied and/or big hipped dinosaurs. So reptiles with small muscles and low blood pressures are not good analogs for giant dinosaurs. Marine reptiles that live in a world that buffers them from gravity are even less so. We find the recent tendency to cite marine and captive reptiles as primary analogs for dinosaurs as unconvincing as it is perplexing. Giant dinosaurs were not good reptiles, or damned good reptiles. They were marvelous archosaurs whose anatomy and aerobics converged with megamammals. It is only logical that the closest living models for extinct land giants are living land

TABLE 2

Size ranges possible with various metabolic systems
in water, land and air

Metabolic Condition & Habitat	Size Range
SEMI-AQUATIC - MARINE	
BRADYMETABOLIC, BRADYAEROBIC - invertebrates, fish, amphibians, reptiles	microscopic - 15 tonnes
TACHYMETABOLIC, TACHYAEROBIC some tuna, sharks, birds, mammals	10 g - 200 tonnes
TERRESTRIAL & AERIAL-	
BRADYMETABOLIC, BRADYAEROBIC - invertebrates, amphibians, reptiles	microscopic - 1 tonne
BRADYMETABOLIC, TACHYAEROBIC larger flying insects	0.2 g - 250 g
Marginal TACHYMETABOLIC, TACHYAEROBIC basal therapsids, brevischian dinosaurs	100 g - 1 tonne
Moderate TACHYMETABOLIC, TACHYAEROBIC derived therapsids, basal mammals, edentates, therizinosaurs? (examples over 1 tonne are TERRAMEGATHERMS)	10 g - 5 tonnes
High TACHYMETABOLIC, TACHYAEROBIC some marsupials, most eutherian mammals longoschian dinosaurs, birds	1.5 g - 100 tonnes

giants with aerobic metabolisms, circulatory systems, and growth patterns suitable for terrestrial gigantism under natural conditions. One way that megadinosaurs differed dramatically from megamammals was in their rapid oviparous reproduction. Combining the latter with HiMR rapid growth produced theropods and sauropods bigger than their mammalian counterparts.

Giant dinosaurs were no more gigantotherms than are elephants. Instead, land giants are "terramegatherms", animals that have or had HiMRs because high aerobic capacity is a prerequisite for evolving body masses over 1 tonne in 1 G. Table 2 outlines the size ranges that can be achieved with various metabolic systems. In water, either low or high MRs work in animals up to 15 tonnes. It is possible that only very fast growing tachyaerobes can become larger in the sea. On land, insects with high active MRs are small because of their decentralized respiratory systems (see Heinrich, 1993; tiny flying insects have adaptations that minimize oxygen consumption). Both low and high MRs work in tetrapods up to 1 tonne, elevated MRs are necessary in bigger forms, and high MRs are probably needed to exceed 10 tonnes.

The anatomical and other evidence indicates that dinosaurian aerobics evolved as follows. MRs started to be elevated above
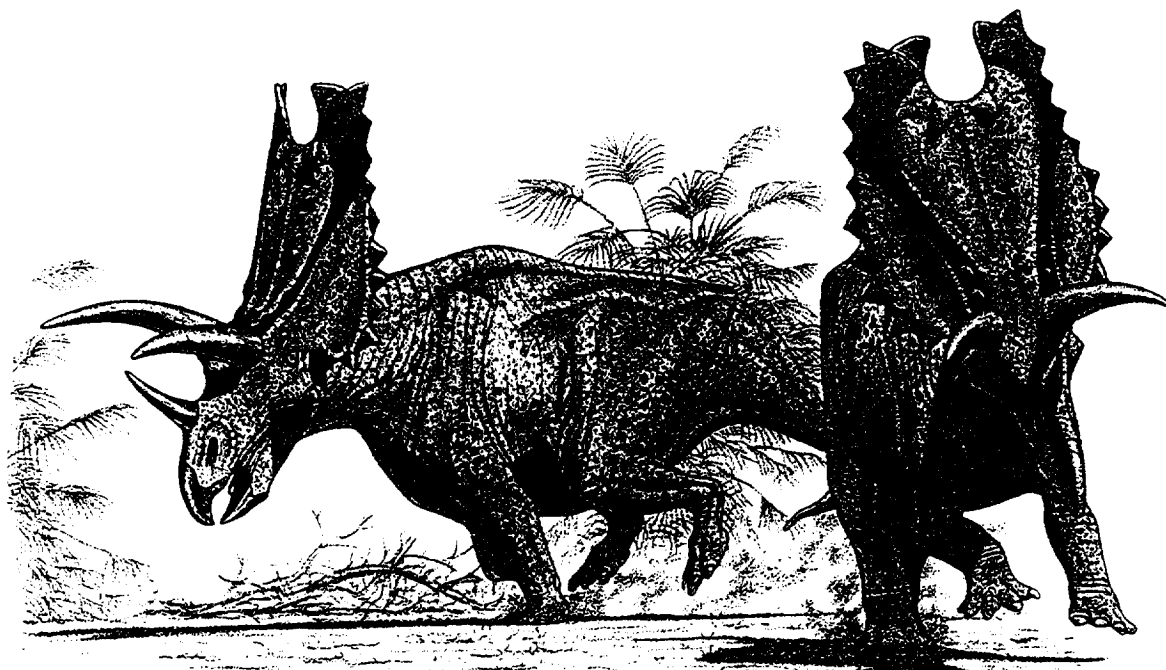
FIGURE 10 - 2.5 tonne <u>Pentaceratops</u> was a classic megadinosaur with long striding legs suitable for fast walking and running, powered by large volumes of tachyaerobic muscles that received oxygen via a high capacity respiro-circulatory system. High metabolic rates were the result of these anatomical features.

reptilian levels in Triassic brevischian dinosaurs. Expansion of the leg muscles to avian-mammalian levels occurred in Late Triassic and Early Jurassic theropods, ornithischians and sauropods. Pneumatic vertebrae indicative of pulmonary air-sacs first appear in Late Triassic theropods and Early Jurassic sauropods. The ornithischian respiratory system evolved in the Late Triassic, and the mammal-like diaphragm of ornithopods evolved by the Middle Jurassic if not earlier. Trackways of fast cruising dinosaurs are imprinted on Late Triassic sediments. Terramegathermic sauropods appeared in the Early Jurassic, in the Late Jurassic sauropods reached 50 tonnes, the biggest 100 tonne examples are found in the Late Cretaceous. Other groups of predaceous and herbivorous dinosaurs also became terramegatherms in the Jurassic and stayed that way until the end. The combined evidence indicates that dinosaurs became tachyaerobic endotherms fairly early in the Mesozoic, and that the MRs of megadinosaurs flat-lined through the rest of the Era, except that the exercise metabolisms of big running tyrannosaurs, hadrosaurs and ceratopsids may have risen a modest amount in the Late Cretaceous. On the other hand, the MRs of ponderous Late Cretaceous therizinosaurs may have declined by a modest amount relative to the more normal Early Cretaceous alxasaurs.

Owen-Smith (1988) stressed the extinction resistance of slow breeding megamammals. It has been little appreciated that even the biggest dinosaurs were prolific "weed species" with much higher recovery potentials than mammals. It is very difficult to

understand how a diverse array of thermally sophisticated Late Cretaceous dinosaurs adapted to living in climates ranging from tropical to polar could have been <u>totally</u> extinguished when environmentally sensitive birds and amphibians survived. This is true regardless of the proposed extinction agent - massive impacts, vulcanism, climatic shifts, marine regressions, oxygen declines, floral changes, etc. The loss of nonavian dinosaurs remains one of the most extraordinary and inexplicable events in Earth History, and may have as much to do with a bad roll of evolutionary chaos as with a specific cause or causes.

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APPENDIX 1: SOME DEFINITIONS

Bradyaerobic: Bradyaerobes have low rates of active oxygen consumption (the reptilian condition).

Bradymetabolic: Rates of oxygen consumption are low under resting conditions (the reptilian condition).

Ectothermic: In ectotherms the majority of body heat is acquired from the environment. These have LoMRs (reptilian condition).

Endothermic: In endotherms the majority of body heat is generated internally. Most examples have HiMRs (avian-mammalian condition), but LoMR giants like leatherback turtles can conserve enough body heat to be endothermic (McNab, 1983; Spotila et al., 1991).

Hyperanaerobic: The very high levels of anaerobic power generated by the muscles of many reptiles.

Tachyaerobic: Tachyaerobes have high rates of active oxygen consumption (the avian-mammalian condition).

Tachymetabolic: Rates of oxygen consumption are high under resting conditions (the avian-mammalian condition).

Apatosaurus as a Means of Understanding Dinosaur Respiration

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INTRODUCTION

Dinosaur activity has been the object of speculation since the first skeletal reconstructions were completed in the last century. Charles Knight, the famous artist, painted dinosaurs as active agile animals whereas researchers later portrayed them as slow moving and clumsy due to some similarities with modern reptiles. Modern research leans toward an active lifestyle for such enormous animals. This implies that dinosaurs needed a lot of oxygen to supply the necessary energy for these activities, but is it possible to estimate just how much this really was? Modern investigations confirm that the ability to supply oxygen to active tissues such as muscle is the factor most likely to set the limits of performance.

Our studies of *Apatosaurus* structure have allowed us to examine and speculate about a number of physical characteristics including its method of breathing, how deeply it could breathe, how often it could breathe and how much oxygen it needed to maintain various activity levels. We have also been able to compare respiratory limitations with metabolic demands and draw some conclusions about its ability to move about in its environment. We also enjoy speculating about lung characteristics and blood characteristics based on what we know about modern animals that are related to dinosaurs: lizards, birds, and crocodilians.

Although *Apatosaurus* is a late Jurassic or possibly early Cretaceous dinosaur, we feel that its thoracic structures are similar enough to those of other sauropods and ornithischian dinosaurs that we can apply our principles demonstrated here to help understand the respiratory mechanisms and limits of these other groups.

WHY *APATOSAURUS*?

Apatosaurus was chosen for study because it was available at the Field Museum, Chicago, Illinois, and because the staff of the Field has graciously allowed us to study and measure its specimen. It was also chosen because as a Diplodocene dinosaur, it has characteristics which allow for physical analysis. *Apatosaurus* shares its family status with another well-known sauropod, *Diplodocus*. Both of these animals have limiting factors that include a small nostril size that limits air intake, a long neck in which air remains at the end of each breath, and a rib-vertebra structure that convinced us that we could analyze breathing capacity.

The small nostril size seen in fossil skulls of *Diplodocus* and *Apatosaurus* probably approximates the actual size in life. For *Diplodocus*, a sister animal to *Apatosaurus*, these openings consist of a pair of wedge-shaped holes 3 cm at the widest part and 8 cm long (Figure 1). The dimensions of *Apatosaurus* nostrils are very similar to those of *Diplodocus* shown in the figure. Other dinosaurs show much larger nostril openings making it difficult to accurately estimate dimensions because these openings might have been lined with soft tissues of unknown thickness. *Apatosaurus* and *Diplodocus* have such small apertures that only a small membrane could have been present and still allowed for air to be moved in any quantity. Nostril openings in an *Apatosaurus* are approximately equal to those of a modern horse but *Apatosaurus* weighed 25,000 kg!
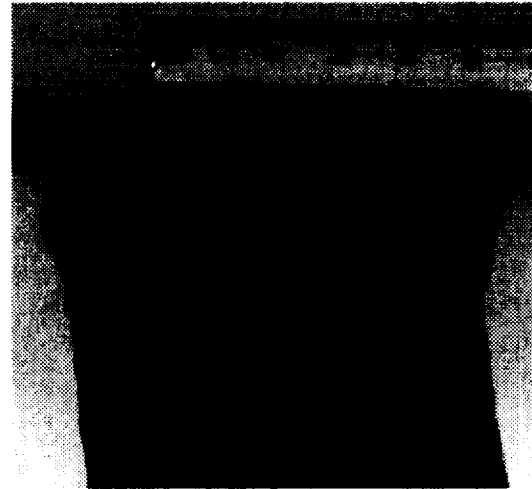
Figure 1
Nostril Size in Diplodocus
(Scale in Inches)

Breathing rates must have been severely limited by the speeds with which large air volumes could be moved through these nostril slits. Hillenius (1992) has demonstrated in mammals that nose-breathing helps conserve water during exhalation as well as the better known function of moistening air during inhalation. Water loss is less in ectotherms than in endotherms but nose breathing is very likely to be advantageous to ectotherms but to a lesser degree than endotherms. Although most animals open their mouth during heavy exertion, nose breathing is preferable during normal activities to conserve water and prevent respiratory tissues from drying. *Apatosaurus* probably had a low metabolic rate closer to ectothermic values than endothermic and could tolerate mouth breathing better than modern endotherms such as

mammals. This tolerance for mouth breathing would become essential during periods of extended exertion when water was not always available as in foraging or migration.

The well-known elongated neck of *Apatosaurus* (Figure 2) was undoubtedly useful in foraging over greater areas without expending the energy to move the entire body. It also presents an interesting problem for physiologists. The air remaining in the trachea or windpipe at the end of each breath requires effort to move it but this air fails to reach lung surfaces. A long neck implies a large volume of unusable air or dead space existed in sauropod dinosaurs. Alternatively, at the end of exhalation, waste gases such as carbon dioxide (CO_2) remain in the trachea only to be re-inhaled at the beginning of the next breath. If the dead space is considerable, the lung is less able to void waste gases. This also has the potential to change the acid-base balance of the body in some circumstances - a very serious problem for many animals and a very interesting one to scientists.

Figure 2
Apatosaurus Showing Elongated Neck
and Nostrils Atop the Head

Finally, the rib and vertebra structure of *Apatosaurus* lead us to believe that a relatively simple method of breathing was used in refreshing the lungs. The air volume moved per breath depends upon the extent of thoracic size changes between the beginning and end of a breath. Volume changes may be through a change in chest dimensions (primarily rib movements) or through internal expansion (movement of organs to the rear of the body) through a diaphragm or similar method. Of the possible means of aspiration breathing, all were eliminated except for expansion of the thorax through rib movements. Therefore, if we could calculate how much and in which direction the ribs moved during breathing, we could estimate the respiratory characteristics of *Apatosaurus*. This simplicity allows for estimates of air volumes moved with each breath and for a comparison of this amount with the needs of the animal during activity.

HOW MUCH OXYGEN DOES A DINOSAUR NEED?

Living vertebrates use oxygen to make energy for everything except the most extreme and temporary activities. A brief burst of activity does not require oxygen; it uses alternative sources for energy. However, the animal must then rest for an extended period while the energy balance is restored - through oxygen. In other words, continuous activities require oxygen (O_2).

Different vertebrates have chosen different strategies in their oxygen usage with very different outcomes. "Cold blooded" animals (ectotherms) demand little oxygen and expend little energy. At times their activities can be very intense and energy demanding. These bursts are also likely to be brief, anaerobic, and require long periods of inactivity to recover. This is because their average needs for oxygen are low and the ability to deliver oxygen is also low.

Endothermic (warm blooded) animals have a high metabolic rate which demands a constant and high level oxygen supply. The more sophisticated oxygen delivery system of endotherms allows for constant and continued energy during activity. In a word, endotherms have more endurance and thus an extended capability for migration, foraging and other sustained activities.

We should ask ourselves whether the metabolic status of the dinosaurs was ectothermic or endothermic. Evidence from dinosaur tracks, migration, and from oxygen isotopes found in fossil bones indicates that dinosaurs may have had a somewhat elevated metabolism, possibly even low levels of endothermy. This further implies that they had greater oxygen demands and more sophisticated oxygen delivery systems than their purely ectothermic ancestors, the reptiles.

Figure 3

Oxygen Consumption in Ectotherms and Endotherms of Similar Size

Bakker (1972) compared the oxygen needs of endothermic and ectothermic animals walking at various speeds. Animals of similar size walking at similar speeds show nearly identical increases in oxygen consumption although their resting values are quite

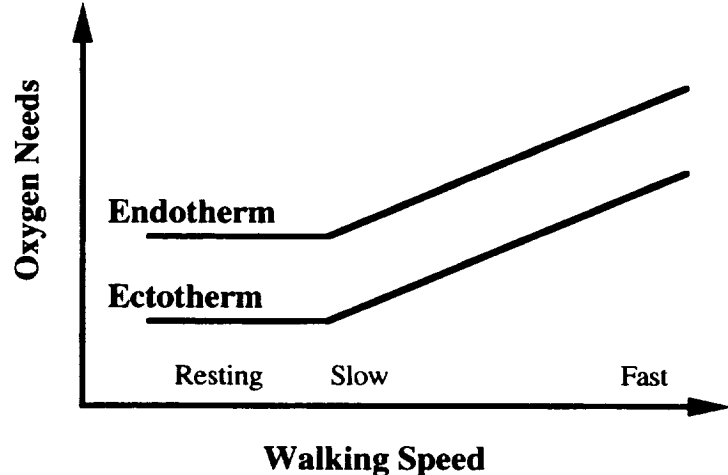different. This is illustrated in the diagram of Figure 3. An endotherm uses more total oxygen because its resting metabolism is higher. In other words, the total oxygen requirement is the amount needed for the effort plus that used for maintenance of the body. Oxygen needed for exercise is determined by body mass. However, the limits of sustained effort will be higher for endotherms because their respiratory systems are better developed to support the ongoing needs for relatively high oxygen delivery.

A variety of factors affect the delivery of oxygen to active tissues. These include the oxygen available in the atmosphere, the volume of air moved per minute to the lungs, the size and thickness of lung surfaces, the oxygen transport capabilities of the blood and the speed with which blood is circulated to the tissues. These factors are diagrammed in Figure 4. Oxygen is around 20.5% (abbreviated to 21% for most discussions) of the total atmosphere at the present. There is some evidence that this may have been considerably higher during the Cretaceous and Jurassic periods when dinosaurs dominated the land. Dr. Gary Landis of the USGS and a member of our research group has analyzed air bubbles trapped in ancient amber. He and co-workers have determined that oxygen comprised from 28% to 35% of the atmosphere during the Cretaceous. If this proves true, then it means that a less efficient respiratory system would have been sufficient for dinosaurs. Our research tends to confirm this prediction at least for *Apatosaurus*. Landis has had access to only a few samples of Jurassic amber to analyze. This simply does not allow for generalized statements about oxygen levels beyond the Cretaceous. However, the few samples assayed so far have indicated that oxygen was elevated during the Jurassic much as it was in the Cretaceous. If this is so, then *Apatosaurus* would have required smaller respiratory movements because each breath delivered more oxygen.

Figure 4
Factors That Limit Oxygen
Delivery to Tissues

DINOSAUR BREATHING?

Breathing or ventilation volumes vary from the minimal volumes needed for resting or low activity levels (Tidal Volume) to the maximal breaths needed to sustain vigorous activity. Each of the tidal values constitutes a fraction of the maximal amount of air

which could possibly be moved in a single breath (Vital Capacity). Thus, some air is always present in the lungs at the end of each breath. This is the residual capacity or volume which is refreshed at varying rates depending upon ventilation depth. Breaths tend to get more frequent with exercise but a limit is quickly reached. Generally, this is accompanied by increased depth of breathing. Depth is important because increases in frequency alone result in reduced time available for inspiration. This, in turn, can actually result in less air reaching the lungs each minute because much of the inspired air is dead space. Thus, there is a finite limit to both the depth and frequency of breathing independent of that associated with the effort simply needed to cause ventilation movements.

We conducted experiments to determine how often *Apatosaurus* could breathe and thus, the maximal volume of air made available to *Apatosaurus* during exertion. A chamber was fitted with a plate in which nostril openings the shape and dimensions of *Apatosaurus'* nostrils as determined from fossil casts. This chamber was then connected to 6.25 meter long tubes with 7.6, 10.2, 12.7 and 15.2 cm diameters. Each tube size was tested in turn on our apparatus. Allowances were made for total lung (chest) volume and for the effect changing chest volume has on lung pressures. Simulated inspiratory pressures were created by a bellows of 250 liters volume. Tests were run with and without nostril plates to simulate physical limits when breathing through nostrils or through an open mouth. As expected, faster inspiration occurred in tubes of larger diameter, and air moved more rapidly when the nostril plate was not present. *Apatosaurus* probably opened its mouth during exertion to increase air delivery just as active animals do today. Tube diameter proved to be a bigger factor in the rapidity of air movement than was the presence or absence of the nostril plate. However, as an air delivery strategy increasing tracheal diameter increases tracheal dead space thus lowering the volume of air delivered per breath. Compensation would require deeper and, therefore, prolonged inspiration times. As an aside, the time needed for expiration is normally the same as or longer than that of inspiration (Leath, personal communication). In all calculations, we have doubled the inspiration time and assumed continuous breathing cycles to estimate the limits of air delivery per minute (minute respiratory volume). Thus, there must be an optimum tracheal diameter at which air delivery is maximized both for depth and for frequency.

Interestingly enough, there was a point beyond which inspiration time was not decreased by increasing inspiratory forces. Attempts to force the bellows at faster rates did not alter the time of inspiration once this point was reached. We believe that the pressure difference that may be achieved between atmosphere and apparatus is finite and that this maximum in combination with airway resistance sets a terminal airway velocity. It is likely that the values we found are generous when applied to air delivery in *Apatosaurus*. Based on our data, we found the most efficient diameter to be between 10.2 and 12.7 cm for air delivery. Based on air flow rates, this allows a maximum of 8-10 breaths per minute at approximately 6 seconds per ventilation cycle (inspiration + expiration).

These calculations required that we know something about vital capacity in *Apatosaurus* if we were to estimate tidal volumes during exercise. Measurement of the internal dimensions of the chest indicated that the cross section could be viewed as an ellipse. *Apatosaurus* has 11 pairs of dorsal (body) ribs which are attached to 11 vertebrae. Careful study of these bones showed major structural differences occurred between ribs 5 and 6 and between vertebrae 5 and 6. Starting from the sixth rib and vertebra and continuing posteriorly, the bones became abruptly less massive and less reinforced. This is what is expected if these bones were subjected to less mechanical stress and movement than the more anterior ribs. Ventilation movements would cause mechanical stress.

The angle at which ribs attach to vertebrae changes progressively from rib 1 through 5. Because each rib attaches at two points to its vertebra, any movement is fixed in a single plane. Ribs 1-3 tend to move anteriorly (forward) while 4 and 5 move progressively more laterally (sideways). This maximizes the efficiency of chest expansion through rib movement and indicates a definite commitment to rib movement in breathing. Some researchers have proposed that bird-like lung systems were present in dinosaurs. Although this cannot be totally ruled out, we saw no mechanical means of ventilating an avian type of respiratory system. We also examined the diaphragmatic ventilation systems of mammals and crocodilians and compared these systems with the problems which would occur because of the presence of extensive abdominal ribs in *Apatosaurus*. Posterior movement of abdominal viscera during inspiratory movement of liver or diaphragm would compress abdominal contents against the ribs. Visceral movement would also be hindered by friction between rib-reinforced walls and viscera. Although such diaphragmatic mechanics cannot be totally ruled out, they were probably less efficient than movement in modern animals. This is because living animals using these mechanisms lack abdominal ribs to affect breathing movements. It is therefore believed that *Apatosaurus* used anterior rib expansion to ventilate as do many lizards. Ruben and others (1987) conducted experiments to determine if mammals (rats) could survive with rib breathing alone. Basic metabolic needs were efficiently served by rib breathing in animals with high oxygen demands. Limitations of rib breathing as a ventilation system were more pronounced during exercise; rats breathing without diaphragms were confined to low levels of activity. In animals with lower metabolic demands, rib breathing is not unduly inefficient.

Apatosaurus's chest has a total volume of about 1580 liters. Of this we estimate that heart and solid lung tissue occupied about 180 liters. Therefore, lung volume was probably near 1400 liters. Maximum distances of respiratory movement were estimated by applying a knowledge of muscle physiology in modern animals, and by measurements of the length of the muscles most likely to have been involved in breathing. The direction of rib movement and the distance of movement were calculated based on the length of muscles which connect each rib to the next. This gave maximal breathing depths of near 330 - 400 liters per breath. Living animals use slightly more than half of their maximum during exercise or about 250 liters. When we applied this to our data for tracheal air

delivery discussed earlier, we were able to derive a value for maximum ventilation per minute. Assuming that tracheal dead space was not excessive, 6.8 breathing cycles move about 1800 liters of air per minute. This would allow *Apatosaurus* a top effort equivalent to 5 km hr^{-1} (5 kilometers per hour) if O_2 were 21%, or 10 km hr^{-1} with 35% oxygen but only if the lung was 100% efficient at extracting oxygen. Although the speeds based on leg length calculations indicate *Apatosaurus* was capable of walking at 6-10 km hr^{-1}, our respiratory data indicate slower maximum speeds were the norm. Using lung efficiency in living animals as a guide, we estimate that *Apatosaurus* was limited to speeds of 4-5 km hr^{-1} and then only if oxygen levels were elevated above 30%. Lockley (1991) has found *Apatosaurus* tracks and calculated the animals were walking approximately 4 km hr^{-1}. Atmospheric oxygen of 21% would limit *Apatosaurus* to speeds of less than that measured by Lockely, probably in the range of 1-2 km hr^{-1}.

Climbing hills must have required massive quantities of oxygen even at slow speeds. Large animals use more energy per kilogram when climbing than do smaller animals (Taylor and others, 1972). Given the relatively small breathing capacity and given the fact that dinosaurs were obviously well adapted to their environment, the simplest explanation of their success is that oxygen was considerably more abundant during the Jurassic than today.

This is not to say that other forms of ventilation could not evolve in a oxygen-rich environment. Skeletal evidence indicates that birds and mammals had evolved the means to ventilate their lungs with air sacs (Britt, personal communication) or diaphragms by the Jurassic (Ruben, personal communication) although some researchers feel that birds may not have all been endothermic at this time (Chinsamy, personal communication). Abundant atmospheric oxygen would have provided an environment in which dinosaurs could flourish without significant respiratory disadvantage to either birds or mammals. We reason that respiration would have become an effective selection factor only after avian and mammalian respiratory systems became quite efficient and only then if atmospheric oxygen declined, and then only if dinosaur metabolism required an elevated oxygen supply. This combination may have occurred near the end of the Cretaceous - when the dinosaurs eventually became extinct.

DINOSAUR LUNGS?

It is also important to consider the surface area of the lungs through which oxygen is extracted and passed to the blood for transport. The greater the surface, the more oxygen that can be exchanged per minute. This is a factor which will never be known since there will never be any living dinosaurs to test and best guesses based on modern animals will have to do.

Crocodilians have the most intricate lung structure of any living terrestrial reptile. Crocodilians coexisted with dinosaurs and are frequently described as their "cousins" in the family tree. Their lungs are distinctly different from those of other reptiles but share

some air passageway structures in common with bird lungs. Most paleontologists believe that birds are descended from carnivorous dinosaurs. It is likely that the common ancestor of birds, crocodilians, and dinosaurs probably also had a lung with many features shared in common. These features include an air distribution system similar to modern crocodilians with a highly partitioned elastic lung. The lung structure in both birds and reptiles requires an active exhalation as well as an active inhalation. It is likely that dinosaurs also breathed in this fashion since they are related to both modern groups. Unless evidence appears to the contrary, the crocodilian-type lung will serve as a model for the dinosaur lung. This is particularly true if we are correct that the ventilation mechanism we have proposed existed in combination with elevated atmospheric oxygen concentrations.

DINOSAUR BLOOD?
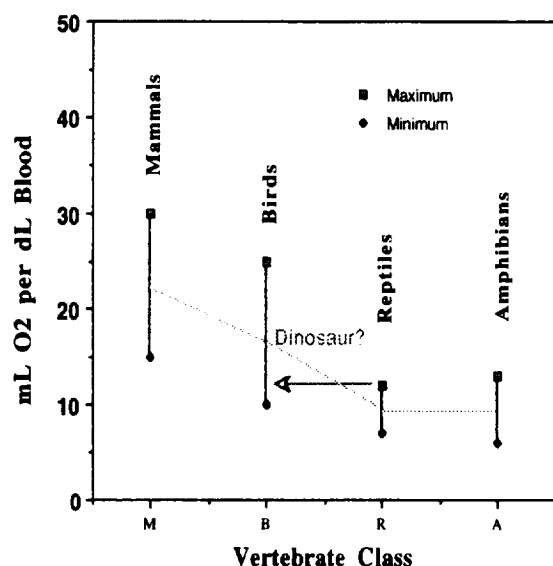
Figure 5
Oxygen Transport Capacity
in Vertebrate Blood

Finally, we must examine the probable characteristics of blood that conducted oxygen to dinosaur tissues. For tissues with high metabolic activities such as muscles, the blood should conduct the largest possible volume of oxygen in the least space. Physiologists term this the oxygen transport capacity of the blood. It is possible to make educated guesses at the nature of dinosaur blood by an examination of the dinosaur's closest living relatives. We reviewed the literature on oxygen transport capacity in terrestrial vertebrates. The data displayed in Figure 5 clarify two points. The first is that animals with smaller blood cells tend to carry more oxygen in a given volume of blood than those with larger cells. The second is that birds and mammals overlap slightly in their oxygen carrying capacity. Because dinosaurs seem to be more closely related to birds and reptiles than to other vertebrates then it is likely that they would also share the blood characteristics of each. This would be in accordance with the oxygen demands of a low level aerobic lifestyle.

We have speculated that dinosaurs may well fit somewhere near the lower oxygen carrying capacity of the avian range and have nucleated red blood cells as do birds and reptiles. There is some evidence from stains found in *Tyrannosaurus* bone marrow that

this may be the situation but at this time, we must await additional investigation and verification that these iron-containing stains are what they appear to be - blood stains.

Large nucleated cells present a number of constraints for *Apatosaurus*. Nucleated cells use oxygen during transport unlike anucleate mammalian cells. In ectotherms this factor is minimal because oxygen demands are relatively low and when body temperatures are low, demands are reduced even more. In birds, circulation time is so short that such cells would have little time to use much oxygen. However, in a large animal such as *Apatosaurus* a significant amount of oxygen may have been used in the extended period of time needed to reach peripheral tissues. If body temperatures were elevated as some authors have proposed, either through retained heat (Spotila and others, 1991) or endothermy (Bakker, 1986) this problem of oxygen usage may have been considerable.

A second factor that should be considered in proposing that dinosaurs had large nucleated blood cells is that the larger cell diameter assocated with this cell type may increase blood viscosity (or resistance to flow) in large vessels. For example, the camel is an unusual mammal in that its blood cells are nucleated. The blood cell count (or cell density) is quite low compared to other mammals of similar size. The reduction in cell numbers is an adaptation that lowers viscosity and allows for normal flow rates in large vessels. Interestingly, erythrocyte size is not a particularly significant factor in capillary blood flow. If our evaluation of the oxygen carrying capacity of various groups is correct, then dinosaurs probably had nucleated blood cells, of a size more similar to that of reptiles than birds.

Finally, any discussion of blood characteristics must consider metabolic demand, lung type and ventilation capacity. High metabolic demand requires efficient lungs, good ventilation mechanisms, and blood capable of transferring large quantities of oxygen per volume of blood. Bird lungs, for instance, are particularly efficient because avian blood quickly extracts a large percentage of the oxygen made available at exchange surfaces through an extensive air-sac ventilation mechanism. High oxygen carrying capacity is consistent with the nature of the system. If we compare this with the oxygen delivery possiblites of blood in a system in which ventilation occurs at relatively low rates, then our scenario is more consistent with dinosaur blood having an oxygen carrying capacity in the range where reptilian and avian blood characteristics overlap.

HOW WOULD DINOSAURS ADAPT TO REDUCED OXYGEN?

Apatosaurus has served us well in our attempts to understand dinosaur respiration and performance limitations. Modern animals vary considerably in their physiological capabilities and their adaptability to environmental stress. One has but to observe mammals or birds of similar body type to see this variety. Dinosaurs surely had a broad span of physiological possiblities. However, although there is great variety in mammal structure, the physiology is reasonably predictable if some allowances are made for adaptations to specific situations. For example, all mammals are endotherms, all have four-chambered

hearts, all have diaphragms, and hormone release evokes predictable responses. The same thing might be said of birds. Reptiles have the greatest physiological variation among living land vertebrates but even in this group generalizations concerning function may be broadly applied with reasonable accuracy. Thus, it should be permissible to make basic assumptions about dinosaur function. At present, we are examining as many (non-theropod) dinosaurs as possible to see how widely the *Apatosaurus* respiratory mechanism applies . It is also interesting to speculate on the effect decreasing atmospheric oxygen would have had on dinosaur adaptation and extinction patterns if our data for sauropods were to apply to a wide variety of dinosaurs. Our very preliminary data as of the time of this writing indicate that all non-theropod dinosaurs examined show similar or modified versions of the ventilation mechanisms described in this paper. The sample is limited to four sauropods (all Jurassic) and eight Ornithischians but lend some credibility to the generalizations that follow.

Data from Landis and others (1993) indicate that oxygen decreased rather quickly in geological terms from 35% to 28% at the end of the Cretaceous. When modern endo therms are confronted with reduced oxygen, adaptation follows predictable strategies. Among mammals and birds, these include increasing the depth of breathing (or possibly thoracic size) and increasing the red blood cell count. (Many more adaptations are also needed to complement these changes but these will not be discussed here.) Dinosaurs had really maximized rib breathing as a mechanism when oxygen was elevated. Landis's data indicate that oxygen declined by about 5-6% in under 300,000 years. By evolutionary standards of animals with long generation times, this is a very brief period to adapt all of the necessary interdependent body systems. Thoracic enlargement accompanied by decreased size is one possible strategy that would require minimal physical disruption. We are presently studying fossil evidence to assess whether such trends actually occurred. For now, we waiting to verify the accuracy of our predictions.

Environmental conditions may have been shifting to select for the more efficient ventilation systems of birds and mammals even with high oxygen demands associated with endothermy. Some demands would have been elevated on the basis of size alone since body temperature tends to be higher in larger ectotherms (Paladino and others , 1990; Spotila and others, 1991). Dinosaurs would have become less able to cope with the increasing seasonality of the times and an increasing need for migration to avoid cooling winter conditions. This does not imply a sudden extinction; rather it implies that fitness was decreasing. Although all vertebrates were presented with decreasing oxygen, birds and mammals were better able to ventilate and extract oxygen while reptiles and amphibians never really used much of it. This situation would have "bought" birds and mammals the time to adapt to the changing conditions.

The second adaptive strategy of increasing red blood cell density to enhance oxygen extraction at the lungs and conduction to tissues is to be considered. If we are correct in our guesses about blood cell size and type, there were also problems inherent in this means of adapting to decreasing oxygen. The nucleated blood cells were probably large

compared with those of modern birds. Increasing blood cell density rapidly increases blood viscosity. Optimum utilization would be through an increase in O_2 transport capacity by reductions in cell size. This increases the number of oxygen transporting cells. Body size may decrease to reduce oxygen losses through blood cell metabolism during periods of transport. These may have shaped the physiology of birds. Mammals have the smallest red blood cells and the highest oxygen transport capacities of terrestrial animals but their lungs are less efficient than those of birds. When the blood of modern birds is tested for oxygen usage, the amount of oxygen removed is greater than mammals. Imagine the problems dinosaurs would have confronted with restricted ventilation, marginally efficient lungs, long circulation times, fairly high metabolic demands and low oxygen carrying capacities. Adaptation had to simultaneously succeed on many fronts if dinosaurs were to survive and continue evolving.

SUMMARY AND CONCLUSIONS

Apatosaurus has sufficient numbers and types of physical constraints on its respiratory system that it has allowed us to estimate much about its physiology and environment. These include breathing rate, depth of respiration, type of ventilation mechanism, probable lung type and some speculation as to its blood type. Many principles from this study may also be applied to other, non-theropod dinosaurs although some factors simply cannot be estimated or known. When this respiratory analysis is extended to speculate upon the effects of decreases in atmospheric oxygen at the end of the Cretaceous, a reasonable explanation emerges for broad patterns of survival and extinction observed in late Cretaceous and Early Tertiary vertebrates.

In this scenario, dinosaurs were committed through evolution to rib movement of the body wall as the means of breathing. Further adaptation of this mechanism was not sufficient to support the levels of metabolic activity necessary for adapting to the changing environment. Increasing oxygen supply by increasing numbers of blood cells was also limited as an adaptive strategy since blood viscosity quickly increases as cell numbers increase. Mammals and birds were not so profoundly affected by decreased oxygen because of the design of their respiratory systems. Maintenance of oxygen delivery was possible and allowed more tolerance of changing conditions and greater time for adaptation. Reptiles and amphibians were not as affected since their metabolic rates are low and did not require oxygen in large amounts.

ACKNOWLEDGMENTS

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Dinosaur Bone Histology:
Implications and Inferences

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INTRODUCTION

A study of the anatomy and morphology of a fossil skeleton indicates the overall size, posture, and form of the animal. Even various functional aspects of the skeleton such as preferred mode of locomotion and chewing mechanisms can be deduced from such studies. But the desire to understand dinosaurs as dynamic, once-living animals and not merely as taxonomic entities arranged in phylogenetic schemes, goes beyond this. In 1842, Sir Richard Owen not only presented dinosaurs taxonomically but he also initiated the quest to understand the biology of these animals. In recent decades, the study of dinosaur paleobiology has blossomed, and has provided a crucial link between studies of morphology (structures) and that of function and physiology.

Several aspects of dinosaur anatomy, ecology and phylogeny have been proposed as indicators of endothermy. Data cited in support of such claims have come from studies of the locomotor apparatus, predator/prey ratios, brain size, ecological energetics, and bone histology. A more recent entrant into the paleophysiology arena is isotopic analysis of dinosaur bone (Barrick et al., 1992), claimed to provide the strongest evidence in support of dinosaur endothermy. Recently, however Kolodny and Luz (1993) have argued that oxygen isotopic compositions ($^{18}O/^{16}O$ or $\delta^{18}O$) reflect paleolatitudes and are the result of diagenetic alterations. Thus it remains true that no single line of evidence compels acceptance of the hypothesis that dinosaurs were endothermic and a general level of skepticism prevails, particularly with regard to very large dinosaurs.

This report provides some basic information on bone microstructure, specific details regarding the nature of dinosaurian bone histology, and includes a discussion of the physiological interpretation of patterns of bone deposition. Furthermore, it demonstrates that although bone histology is not directly correlated with thermoregulatory status, it does, nevertheless, provide pertinent insights into the complex questions of bone depositional rate, overall growth rate, and growth strategy.

STRUCTURE OF BONE

In living animals bone is a living tissue comprising a heterogenous mixture of organic and inorganic components. The inorganic material is composed of a poorly crystalline hydroxyapatite ($Ca_5(PO_4)_3OH$) while the organic material is mainly collagen and a composite of various proteins and mucopolysaccharides. Upon death and burial of the animal, the degree of preservation of the various bone components is a function of time and environmental factors. The organic components generally decay while the crystalline apatite and the amorphous inorganic phases are more resilient. There have, however, been reports of proteins, amino acids and fatty acids recovered from fossil hard tissues. For example, Bocherens (1991) has reported collagenic amino acids from *Anatosaurus*, a Maastrichian hadrosaur, while Pawlicki (1979) has reported mucopolysaccharides in *Tarbosaurus*, a carnosaur from the Cretaceous of Mongolia.

The spatial organization of the organic components (particularly collagen) determines the spatial organization of the apatite crystals (Ricqlès, 1991). Thus in fossil bone, even though the organic material is rarely preserved, the histological structure can still be deciphered as a direct result of the once close association of the organic and inorganic components.

At a gross macroscopic level a cross section or longitudinal section of a long bone, such as a femur, humerus, or tibia, clearly reveals two types of bone: the compact bone wall and the inner cancellous or spongy bone which surround the hollow medullary cavity. Both are distinguishable with the naked eye. Compact bone is a solid mass of bone which is cellular and generally well vascularized depending on the species. The individual bone cells, termed osteocytes, have numerous processes called canaliculi which ramify throughout the bone forming an intercommunicating network (for nutrients etc.). The vascular canals have variable orientations and often display anastomoses between neighboring vessels. Vascular canals can have a simple arrangement or can be enclosed within bony structures called osteons.

The structure of the primary compact bone provides the most valuable insight into growth. Since bone is a living tissue, the microscopic structure of bone provides a reflection of growth rates; overall body growth rate determines the nature of the bone structure (Amprino, 1947). The organization of the fibrillar matrix provides an indication of the relative rate of bone formation. Fibro-lamellar bone with its randomly organized matrix, is formed when osteogenesis is rapid, while lamellated bone, with its more organized matrix, is formed when bone accretion is slow (Amprino, 1947). If the primary compact bone is stratified by alternating bands of bone forming growth rings (i.e. a zonal arrangement), it suggests that osteogenesis, and hence growth, occurred in a cyclical or interrupted manner. The absence of zonation implies that growth was continuous (Figure 1).

Typically mammalian and bird bone shows highly vascularized, azonal Fibro-

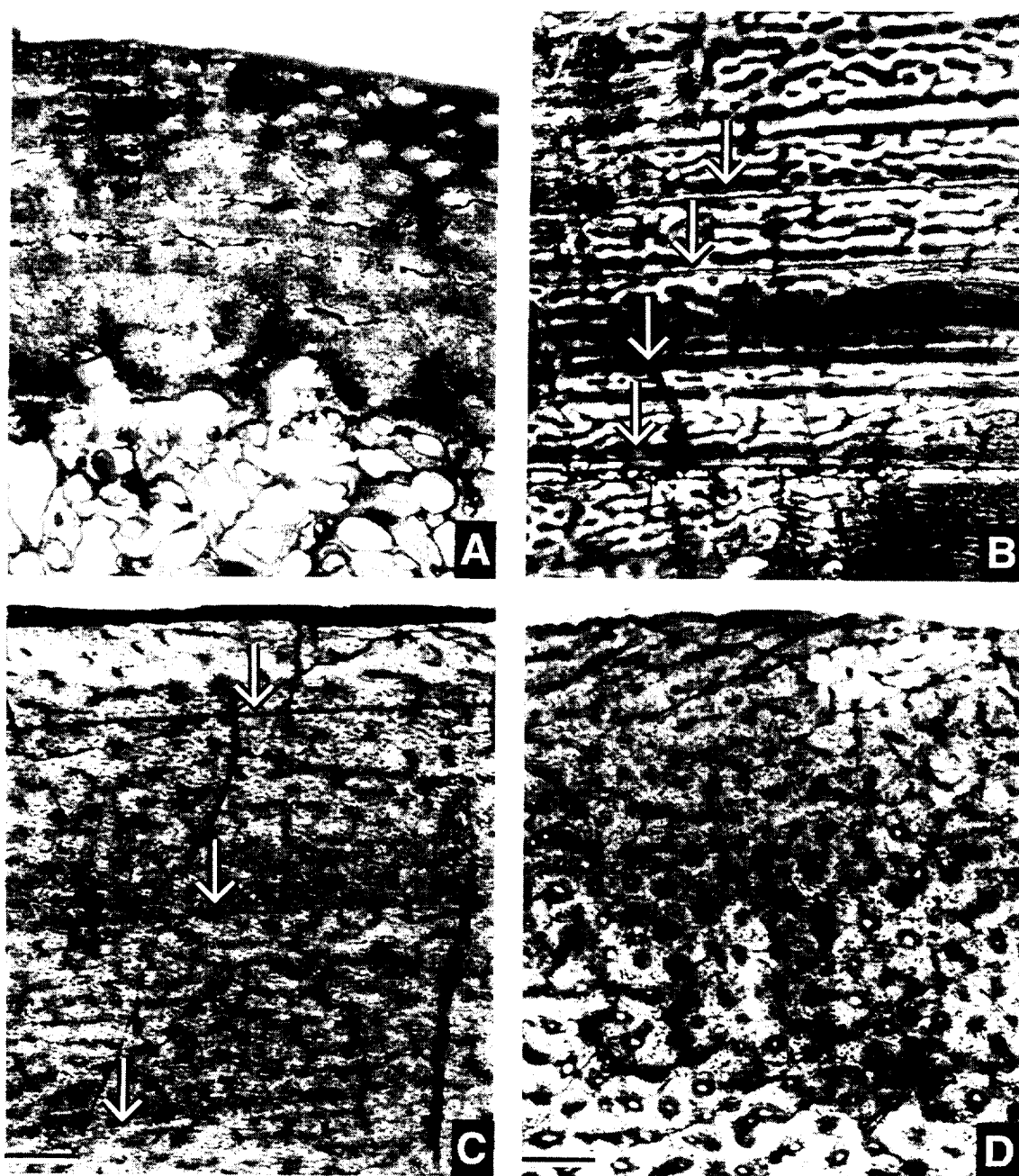*Figure 1- A,* Lamellar-zonal tissue of *Crocodylus niloticus.* Femur (Za 905Ra), transverse section (t.s.). *B,* Zonal bone of an adult *Massospondylus carinatus.* Femur (BP/I/5241a), t.s., 40X. Arrows indicate LAGs. *C,* Zonal bone in *Postosuchus.* Arrows indicate LAGs. Femur, t.s., scale bar= 0.21mm. *D,* Fibro-lamellar bone in *Dryosaurus lettowvorbecki.* Femur (13711), t.s., Scale bar = 0.21mm.

lamellar bone tissue. In mature individuals, closely spaced rest lines may be deposited in the peripheral regions of the compacta that indicate a slow rate of osteogenesis and the determinate nature of growth in these animals. The compacta of reptiles is generally poorly vascularized and typically composed of lamellar-zonal tissue (Enlow, 1957; Figure 1A). Narrow bands of lamellated annuli (sometimes associated with lines of arrested growth (LAGs) which mark distinct pauses in osteogenesis alternate with wider regions termed zones, generally comprised of lamellated bone. Much research has attempted to interpret the causes of such cyclicity in reptilian bones. By examining reptiles of known ages treated with tetracycline (fluorescent dye), scientists have confirmed that the cycles are annual and that the annulus is formed during the unfavorable season whereas the zone is deposited during the favorable growing season (e.g., Castanet and Cheylan, 1979). Furthermore, even reptiles grown in crocodile farms under optimal conditions (Chinsamy, 1991), as well as those living naturally in aseasonal environments (Patnaik and Behera, 1981), still form such growth rings. By applying the technique of skeletochronology (e.g., Castanet et al., 1988), which involves counting the number of growth rings, the age of the animal can be deduced.

The term haversian bone is frequently used in discussions of dinosaur physiology (Ricqlès, 1980; Bakker, 1986). This type of bone is the result of a process termed haversian reconstruction, secondary reconstruction, or substitution; bone surrounding primary vascular canals is resorbed to form enlarged cavities. After resorption ceases, centripetal deposition of lamellar bone occurs and refills the cavity to form a secondary osteon. Secondary osteons are distinguishable from primary osteons because they are bound by a distinct line, termed the cementing or reversal line, which marks the furthest extent of bone resorption (Figure 2B). Early in the reconstruction process, a few secondary osteons may be separated by wide areas of primary bone. Successive generations of secondary osteons may form in the same location, resulting in dense haversian bone, where even the bone between secondary osteons is secondary. Haversian reconstruction is well understood as a histological process, although there is no consensus as to its biological meaning. Several propositions have been made including metabolic starvation resulting from damage to the vascular system, necrosis of osteocytes, and biomechanical adaptation to physical strain. The consensus opinion is the hypothesis that bone, besides supporting the muscles and soft tissues and allowing for locomotion, functions very importantly in phosphocalcic metabolism.

Bone remains a dynamic living material throughout the lifetime of an individual, and thus provides a direct record of the growth processes that characterized the life history of the now extinct animal. It is these facts that makes the study of fossil bone so enticing.

DINOSAUR BONE HISTOLOGY

Dinosaur bone histology is a field that is currently gaining much enthusiastic attention, although in fact the study dates back to the latter part of the nineteenth century. These and subsequent studies laid the framework for the comparative approach that is so valuable today.

Several studies (Gross, 1934; Enlow and Brown, 1957; Currey, 1960, 1962; Ricqlès, 1980) have shown that in some respects dinosaur bone histology resembles that of mammals and is strikingly unlike that of extant reptiles. As a direct result of such similarities, the characteristics of high vascularization and the occurrence of fibro-lamellar, and haversian bone were frequently cited to support hypotheses of tachymetabolic endothermic dinosaurs (e.g., Bakker, 1986). Such claims were made despite the fact that no causal relationship among tachymetabolic endothermy, high vascularity, fibro-lamellar bone, and haversian reconstruction exists. Each of the histological characteristics mentioned can be recognized in ectotherms and in some cases are absent in known endotherms (e.g., Reid, 1987).

Dinosaur bone is indeed very well vascularized (Figures 1B, 1D, 2A). Currey (1962) reported that the bone of an unidentified prosauropod was as highly vascularized as modern artiodactyls. Recently, using morphometric image analysis techniques, Chinsamy (1991, 1993b) determined that the femora of the Early Jurassic prosauropod *Massospondylus carinatus*, of the South African Red Beds, was more vascular than those of the extant ostrich, *Struthio camelus*, and the secretary bird, *Sagittarius serpentarius*. Femora of the Zimbabwean Early Jurassic theropod, *Syntarsus rhodesiensis* was as vascular as the similarly sized secretary bird and considerably more vascular than the crocodile, *Crocodylus niloticus*, which had the least vascular bone of all the species studied. Furthermore, Chinsamy (1993b) also determined that the bones of all the juvenile species examined were much more vascular than the adults of the same species. When attempting to quantify the vascularity of bones it is imperative to consider the nature of the primary bone; that is, whether it is fibro-lamellar or lamellated, and whether simple vessels, primary osteons, or secondary osteons occur (Chinsamy, 1993b). Secondary osteons in dinosaurs were first recognized by Gross (1934) in the prosauropod *Plateosaurus* and the sauropod *Brachiosaurus*. Since then, secondary osteons and dense haversian bone have frequently been recognized in dinosaur bones (e.g., Ricqlès, 1980). Assuming that bone resorption and centripetal bone accretion occurs at a rate similar to mammals, Chinsamy (in press) deduced that in a juvenile of *Dryosaurus lettowvorbecki*, a Late Jurassic ornithopod dinosaur, 80 days were required to form a secondary osteon (average width 143.5μm, and a average bone wall thickness of 42.1μm). Thus, she proposed that the particular individual was at least 80 days old or perhaps even older, because the onset of secondary reconstruction is known to be delayed in some species, suggesting that there is a period before which no secondary haversian reconstruction occurs.
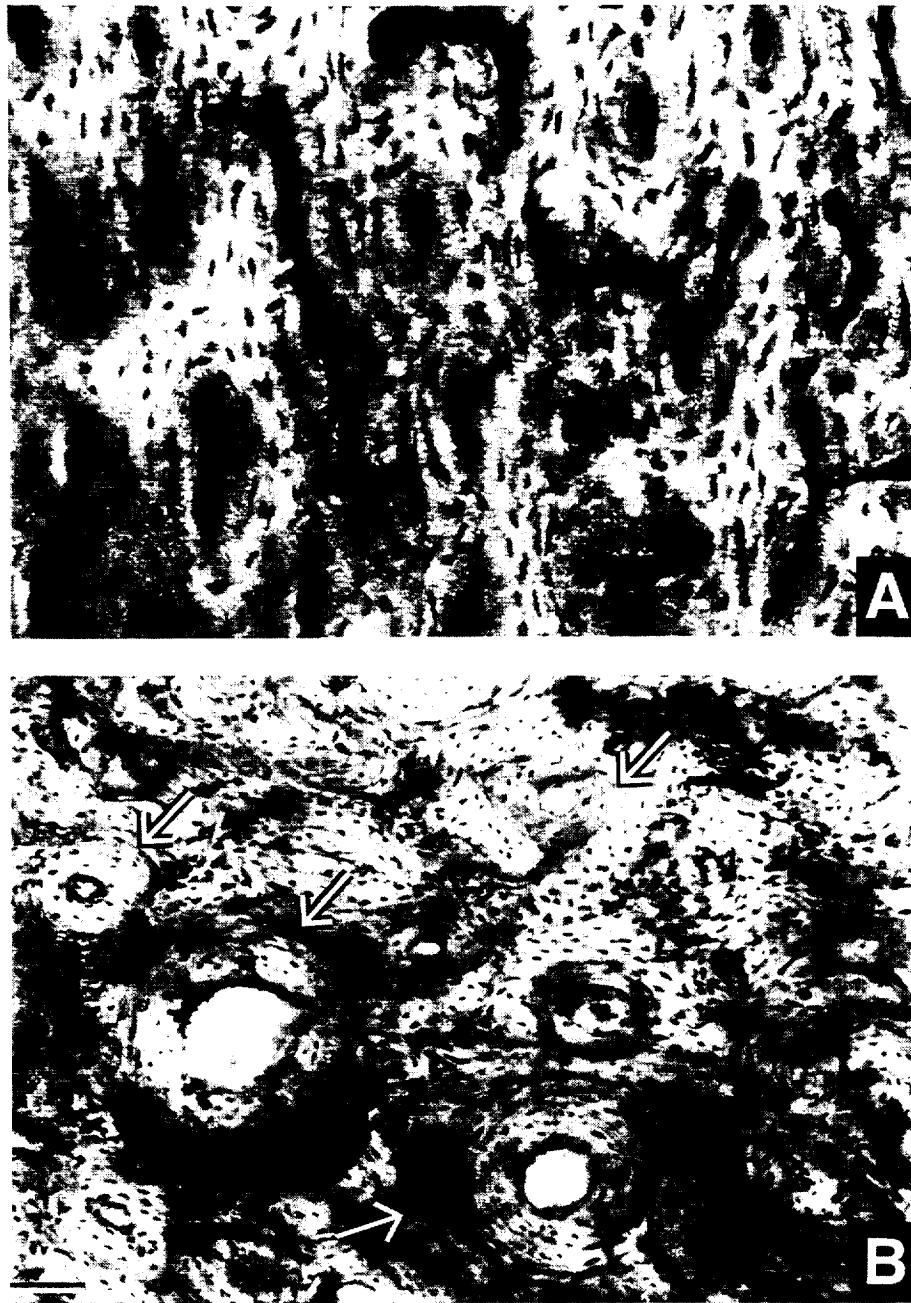
Figure 2- A, Fibro-lamellar bone of *Syntarsus rhodesiensis.* Femur (CT6), t.s., 1080X. *B,* Secondary osteons (arrows) in the compacta of *Dryosaurus lettowvorbecki.* Femur (GPIT/13711), t.s. scale bar = 0.085mm.

Fibro-lamellar bone (Figure 2A) was long considered to be a feature typical of endotherms (mammals and birds) and the frequent occurrence of this tissue in dinosaur bone led to the inference of an endothermic physiology for dinosaurs (Bakker, 1986). However, such tissue is now also known to occur in bones of juvenile crocodiles grown in commercial crocodile farms (Buffrénil, 1980) and in *Alligator mississipiensis* found in the wild (Reid, 1993). Furthermore, such tissue has been documented in pelycosaurs (Enlow and Brown, 1957), cotylosaurs (Enlow and Brown, 1957), dicynodonts (Gross, 1934; Ricqlès, 1976; Chinsamy and Rubidge, 1993), and gorgonopsians (Ricqlès, 1976), all of which are mammal-like reptiles (therapsids) and are generally not regarded as endotherms. Thus, the occurrence of fibro-lamellar bone does not signify ectothermy or endothermy but does unequivocally record rapid rates of bone deposition (Reid, 1990).

Reptiles that form fibro-lamellar bone typically do so periodically. Fibro-lamellar tissue deposited in the zonal regions of their compacta is generally followed by a layer of lamellated tissue and/or a line of arrested growth (LAG). This cyclical formation of fibro-lamellar bone contrasts sharply with the pattern found in mammals and birds which are capable of depositing fibro-lamellar bone without any interruptions or pauses in the rate of bone deposition (i.e. without lamellated bone and associated LAGs).

For a long time it was generally believed that all dinosaurs exhibited uninterrupted fibro-lamellar bone typical of mammals and birds. However, in 1981 Robin Reid astounded the paleontological world by demonstrating fibro-lamellar bone with distinct interruptions in growth by lines of arrested growth (LAGs) in the pelvis of a Mid-Jurassic sauropod. Subsequently Ricqlès (1983) reported cyclically formed bone in the humerus of the sauropod, *Bothriospondylus*. Confronted with such evidence, proponents of dinosaurian endothermy reasoned that such zonal bone was a peculiarity of sauropods only and generally quite rare among other dinosaurian groups. However, in a follow-up paper Reid (1990) demonstrated that zonal bone is fairly widespread throughout the Dinosauria. Furthermore, Chinsamy (1990, 1993a) has shown the occurrence of growth rings in ontogenetic series of two species of southern African dinosaurs, *Massospondylus carinatus* (Figure 1B) and *Syntarsus rhodesiensis* (Figure 3).

PHILOSOPHICAL FRAMEWORK OF ONTOGENETIC STUDIES

Until recently, studies on dinosaur bone histology were based on isolated single bones. Because histological variability between different skeletal elements and within single bones has been documented, the histology of isolated single specimens should not be considered representative of the species. Bone bed material with an assortment of anatomical remains is suitable for documenting the variability of tissue types in the skeleton but is not suitable for comparative studies considering ontogenetic growth.
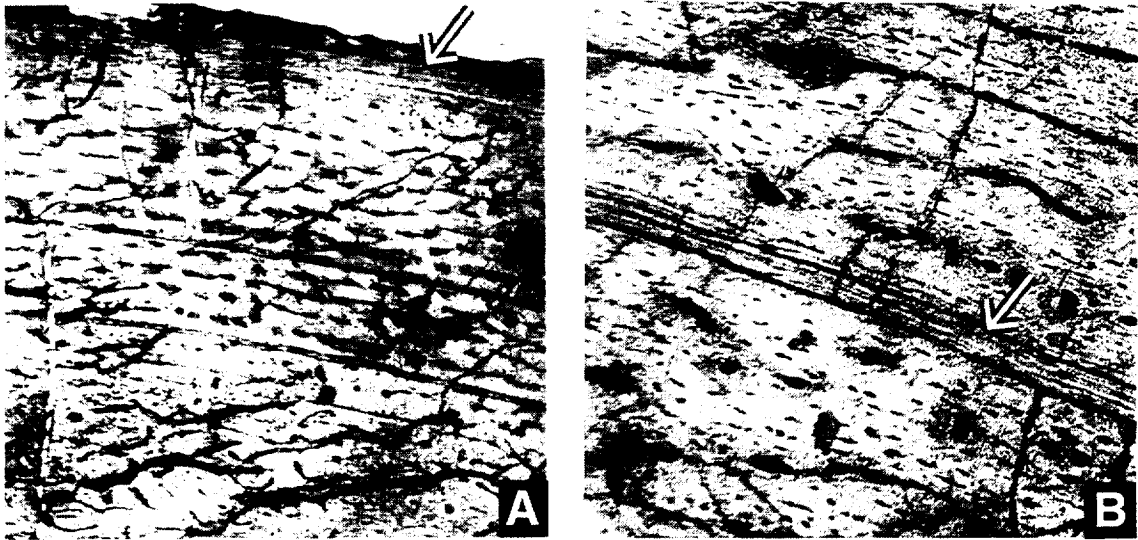
Figure 3- A, Growth rings and peripheral rest lines (arrow)
in Syntarsus rhodesiensis. Femur, t.s., 40X. B, A high
magnification of an annulus (arrow) and zones of Syntarsus
rhodesiensis. Femur, t.s., 520X.

Thus one cannot purport to study growth by sampling a rib of a embryo, a femur of a
juvenile, and a tibia of an adult. Assembling a skeleton from a bone bed is not the
equivalent of studying a single individual because only in the latter case have all
skeletal elements experienced the same internal and external factors. The ideal
situation would be to examine complete skeletons of ontogenetic series of species. In
this way the ontogeny of each skeletal element can be traced, variability throughout
the skeleton documented, and physical and biological stresses or signatures in
individuals interpreted. This ideal, however, is highly improbable because curators
are understandably reluctant to permit comprehensive sectioning of even a single
complete skeleton let alone a series of skeletons. In fact, not even a single
dinosaurian skeleton has ever been sampled comprehensively let alone an ontogenetic
series of skeletons. Considering these circumstances, the best available option is to
standardize the study by examining homologous elements of animals of different
ontogenetic stages. Long bones such as femora are preferred over the highly
remodeled ribs, pelves, shoulder blades, jaw bones and other skeletal elements.
Furthermore, some skeletal elements are known to stop growing at an earlier stage
than overall body growth (Castanet, 1988). Chinsamy (1990, 1991, 1993a, 1993b, in
press) has chosen to examine long bones, especially the femur, and to compare the
histology in the midshaft region, the neutral zone which is the area least affected by
remodeling changes.

INTERPRETATION OF PATTERNS OF BONE DEPOSITION

Studies of growth series of femora of taxonomically well defined species of dinosaurs (Chinsamy, 1990, 1993b) have suggested that the growth rings consisting of alternating deposits of fibro-lamellar bone and lamellated bone were formed annually, because there is no other cycle known to produce such a pattern and because the number of growth rings increases steadily with increasing femoral size. Chinsamy's study sample (1990, 1993b) consisted of 17 femora ranging in length from 12cm to 44cm for *Massospondylus*, a prosauropod, while the sample size for a ceratosaur, *Syntarsus*, was 12 femora ranging from 12cm to 23cm in length. By applying skeletochronology to the growth rings in the compacta of both dinosaurs she determined growth curves for each by plotting the number of growth rings versus femoral length (Figure 4).

The determination of these growth trajectories marks an important step in dinosaur paleobiology, because longevity and growth rate have been the subject of much debate. It has been speculated that some dinosaurs took several decades to reach maturity while, at the other extreme, there have been speculations that dinosaurs matured within a single year. Dunham et al. (1989) have postulated that the slow growth rates extrapolated from living reptiles would be highly improbable because this would require extremely high juvenile survivorship rates. Considering the nature and magnitude of various demographic and physiological factors that must have constrained life history variation, they concluded that a more reasonable estimate for growth to adult size for large hadrosaurs and other large dinosaurs would be 10-12 years. These estimates of growth rates in dinosaurs were based on theoretical modeling. Now, for the first time, growth rates of dinosaurs can be directly ascertained from characteristics of their bone tissue. Chinsamy (1990, 1993a) proposed that *Syntarsus* required 7 years to reach maximum body size and *Massospondylus* took about 15 years (Figure 4). Indeed these are rather slow growth rates and they challenge the notion of fast-growing endothermic dinosaurs.

The growth curves suggest that both dinosaurs experienced fairly rapid growth initially, and that later in ontogeny growth rates slowed. The histological evidence supports this general conclusion and, furthermore, allows more specific deductions regarding growth trajectories. The occurrence of distinct closely-spaced rest lines in the periphery of the compacta of *Syntarsus* suggests that growth had virtually ceased (Figure 3A). Thus it appears that *Syntarsus* experienced a determinate growth strategy as do mammals and birds. The theropod *Troodon* (Varricchio, 1993) and an unidentified theropod dinosaur (Reid, 1993) also show closely spaced rest lines. Other evidence for determinate growth in dinosaurs has come from the evidence of avian-like growth plates in juveniles of *Maiasaura* (Barreto et al., 1993). The largest femora of *Massospondylus* and *Dryosaurus* do not show any closely spaced rest lines in the peripheral regions of their compacta, suggesting that they experienced an indeterminate growth strategy, as do extant reptiles.
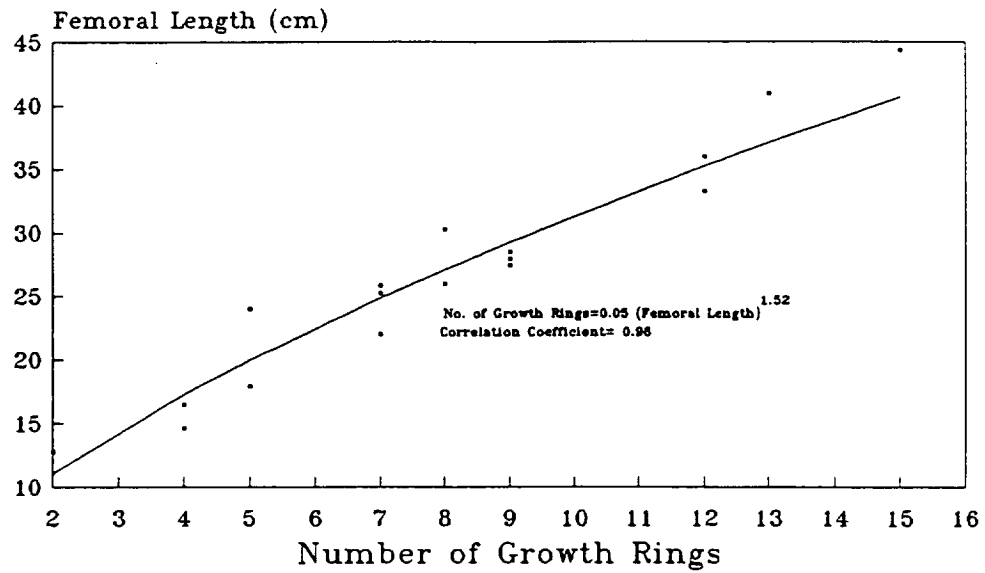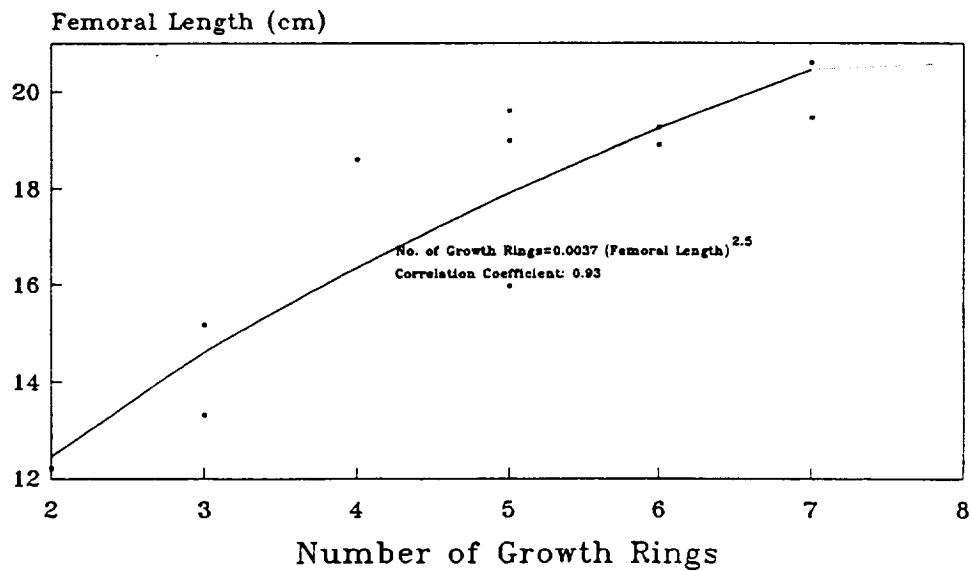
Figure 4- Predicted growth curves. *A, Massospondylus carinatus. B, Syntarsus rhodesiensis.* The dotted line reflects the determinate nature of growth as reflected by the bone histology.

Preliminary studies of the bone histology of femora of growth series of *Coelophysis* and *Protoceratops* reveal that they have highly vascularized fibro-lamellar bone with periodic interruptions in osteogenesis (Figures 5A, 5C). Figure 5B illustrates the cancellous nature of a juvenile *Protoceratops* femur. *Pachyrhinosaurus* samples also show fibro-lamellar bone (Figure 5D) but here LAGs and rest lines appear only late in ontogeny. Such interruptions in the rate of bone deposition imply that these animals were unable to maintain a high sustained rate of bone deposition throughout their lives.

A recently completed study of 13 femora of a medium-sized ornithopod, *Dryosaurus* (Chinsamy, *in press*) from the Late Jurassic Tendaguru beds of Tanzania, revealed fibro-lamellar bone formed continuously without any interruptions or pauses in the rate of deposition (Figure 1D) as occurs in extant mammals and birds. These findings immediately suggest some physiological difference between *Dryosaurus* and the other dinosaurs studied. Could *Dryosaurus* have been an inertial homeotherm? This seems highly unlikely. If *Dryosaurus* had been a large animal mass effects could have played a role in maintaining a high body temperature. But, being comparatively small and weighing only about 70kg, it seems to have maintained a high body temperature by endogenous means. However, unlike typical modern mammals and birds, the largest individual of *Dryosaurus* does not appear to have stopped growing (i.e., they experienced an indeterminate growth strategy). This sort of mosaic of mammalian and reptilian bone histological patterns among *Dryosaurus*, *Syntarsus*, and *Massospondylus* suggests that dinosaurs were neither typical ectotherms nor typical endotherms, but that they employed specialized and perhaps different physiological strategies.

CONCLUSION

What does bone really tell about the physiology of extinct animals? Bone certainly does not provide any foolproof indication of whether dinosaurs were endotherms or ectotherms. The fact that a variety of types of histological patterns are found among the Dinosauria, and that mosaics of tissue structures typical of extant ectotherms and endotherms occur, indicates that such categorizations are quite arbitrary. Although the exact nature of the thermal strategy of dinosaurs still eludes us, the histological structures suggest a intermediate physiology between classic ectothermy and endothermy, perhaps specializations of endothermy (e.g., heterothermy) or even of ectothermy (e.g., inertial homeothermy, gigantothermy). Furthermore, the evidence suggests that there is no single thermal regulatory strategy unique to the Dinosauria, but that differing strategies occurred.

Although it is true that there is no strict causal connection between bone histology and thermal strategy or metabolic rates, studies of bone microstructure does provide unbiased indications of bone growth and inferences of overall rates of growth. Thus,
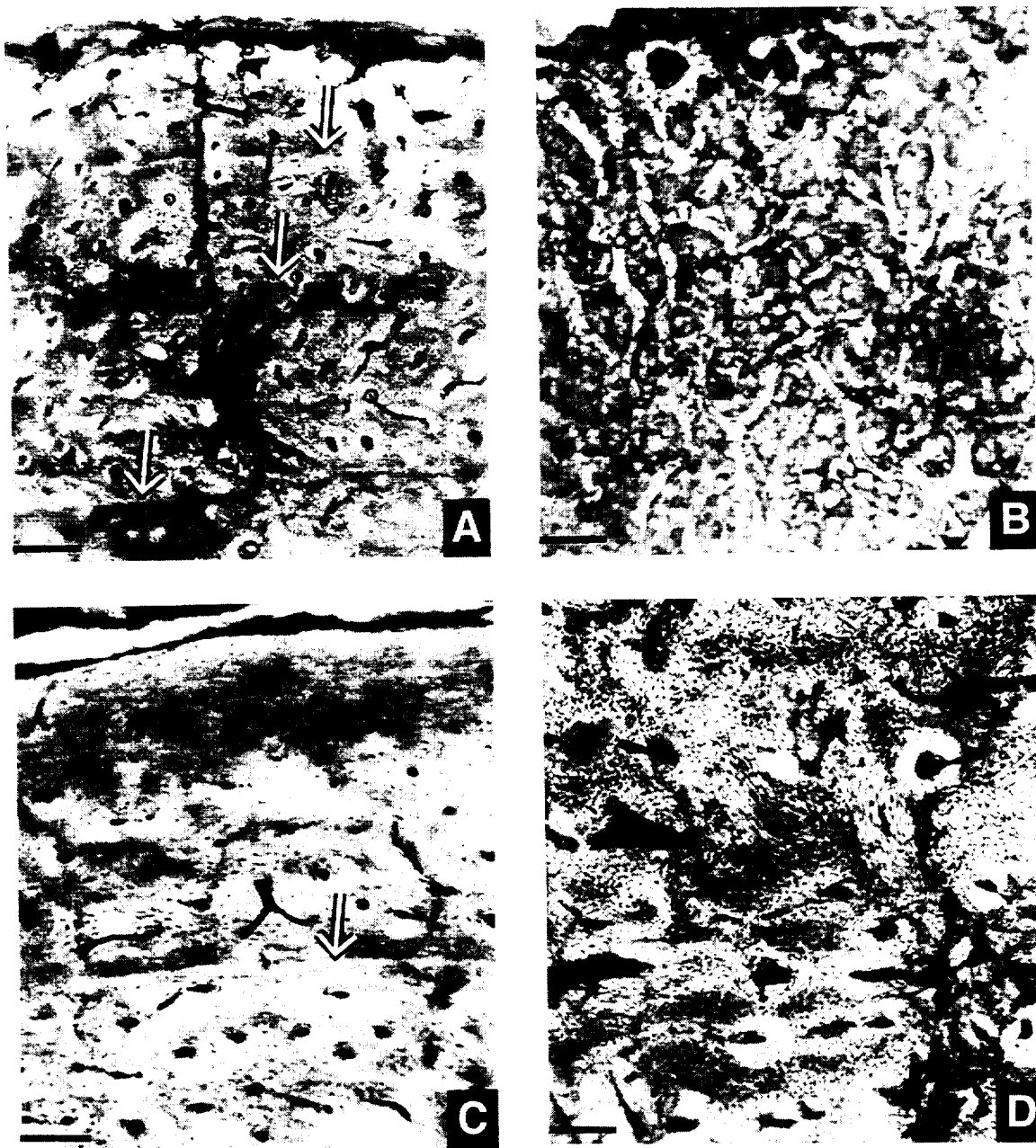
Figure 5- A, Zonal bone of *Protoceratops andrewsi*. Arrows
indicate LAGs. Femur, t.s., scale bar = 0.21mm. *B,*
Cancellous nature of a juvenile *Protoceratops* femur. T.s.
Scale bar = 0.21mm. *C,* Arrow indicates a LAG in *Coelophysis
bauri*. Tibia, t.s., scale bar = 0.21mm. *D,* Primary and
secondary osteons in the compacta of *Pachyrhinosaurus*.
Femur, t.s., scale bar = 0.085mm.

properly constrained, bone histology studies promise a privileged and powerful insight into dinosaur biology that is free of *a priori* assumptions. Furthermore, because bone histology is not based on theoretical models with ambiguous application to the living world but rather on direct evidence from the fossils, its contribution to paleobiology is compelling.

ACKNOWLEDGEMENTS

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Paleoneurology:
Reconstructing the Nervous Systems of Dinosaurs

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INTRODUCTION

The most tangible clues to the existence and lifestyle of extinct vertebrates are the fossilized bones preserved in sedimentary rocks. During the past two hundred years, scientists have excavated, prepared and reassembled the often fragmentary remains of dinosaurs, enabling them to reconstruct the size, proportions and general anatomy of these Mesozoic reptiles. However, the information available from the bones is not restricted to details of the hard tissues themselves. Bone is a living tissue that interacts with the soft tissues of the body and retains evidence of this interaction after death. As a result, paleontologists are able to use preserved bones and other hard tissues to predict traits of physiological processes and of soft tissues. Prime examples of this approach have been the attempts to predict the thermal regime of dinosaurs. Histological structure of bone has been shown to vary with thermal regime in living vertebrates (Ricqles, 1976; Reid, 1987), and the preserved fine-structure of fossilized dinosaur bone has allowed direct comparison with the bone of living vertebrates. Other examples of reconstruction of lifestyle and soft tissues from bony remains include use of the muscle scars on dinosaur bone to predict size and orientation of muscles (Gatesy, 1990), and of dentition and jaw geometry to predict dietary regime (Weishampel and Norman, 1989).

The nervous system may seem to be a particularly inappropriate subject for paleontological analysis: no trace of the original tissue is ever preserved in the fossil record, and most of the system's complexity is cellular in nature. However, the great importance of the nervous system to the life of the animal has resulted in an intimate system of bones that protect and support it. These bones are often preserved and allow reconstruction of the nervous system's gross anatomy, which reflects its cellular anatomy to at least some extent. Furthermore, because the nervous system is the means by which an animal senses and responds to its environment, it is a sensitive and powerful indicator of lifestyle.

A critical step in predicting dinosaur lifestyle in this manner is a general understanding of the relationship between the nervous system and lifestyle in

living relatives of the extinct dinosaurs. As a result, a large portion of any project is a description and analysis of the nervous system of living lizards, crocodilians, and/or birds.

SUMMARY OF NERVOUS SYSTEM ORGANIZATION

Living reptiles. — The excitable cells of the nervous system, called neurons, are capable of transmitting information throughout their length. Information is passed between neurons at synapses, which are numerous and which vary in type and in effect. It is the large number of neurons and the complex pattern of synapses between them that provide the complexity for which the nervous system is famous.

In gross organization, the nervous system of all vertebrates may be subdivided into peripheral and central nervous systems. The peripheral system carries information to the central nervous system from sensory receptors (sensory neurons) and from the central nervous system to effector cells (motor neurons). Both sensory and motor neurons are incorporated into the segmental nerves, each of which exits between adjacent vertebrae to service a segment of the body (Fig. 1). Segmental nerves exiting at limb

cervical vertebrae

brachial enlargement

brachial plexus

dorsal vertebrae

lumbosacral enlargement

lumbosacral plexus

sacrum
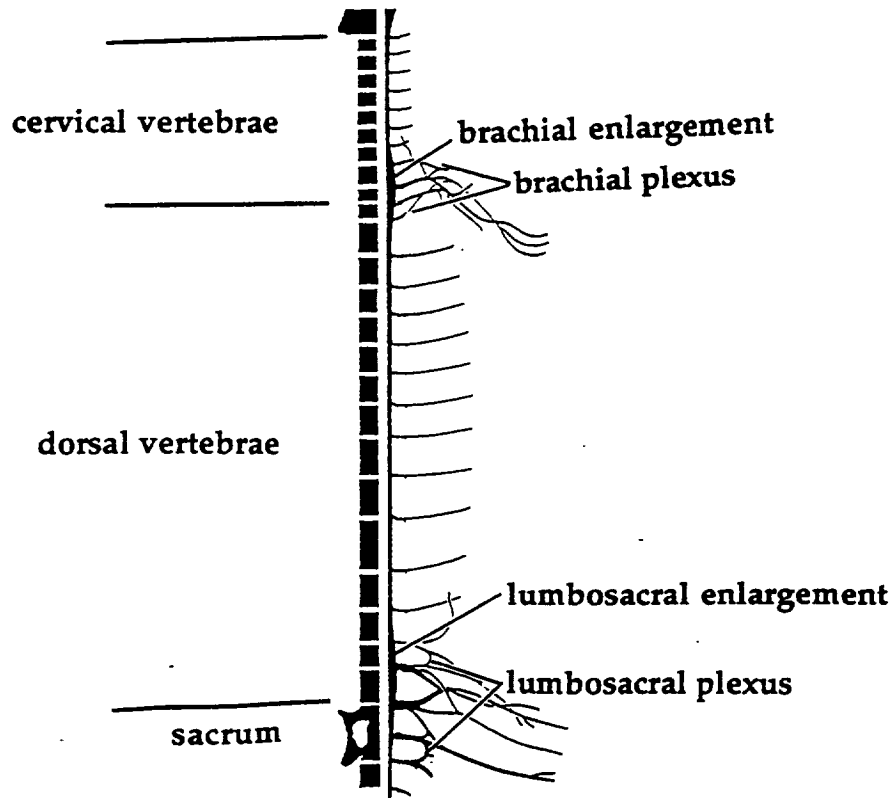
Figure 1. Gross organization of the spinal cord of *Alligator*, shown in relationship to vertebrae. Modified from Giffin (in press a).

levels are typically unusually large, reflecting the increased areas innervated, and interweave to form complex plexuses that supply the arm (brachial plexus) and the leg (lumbosacral plexus).

The central nervous system consists of the spinal cord and brain, and acts as the bridge between incoming sensory and outgoing motor impulses. The cord varies in shape and in cross-sectional area along its length, as the number of neurons supplying a given body segment increases or decreases (Kusuma et al., 1979). Connections mediated at the level of the spinal cord are involuntary, and are termed reflexes.

The brain contains centers for the reception and processing of information from a variety of sources, including from the "special sense organs", the nose, eye, and ear. Areas receiving input from each of these special senses are recognizable externally in the brains of living reptiles as the olfactory lobes, optic lobes, and cerebellum respectively (Fig. 2). The cerebrum is the primary integration center of the brain, and its relative size may be correlated generally with degree of behavioral flexibility.
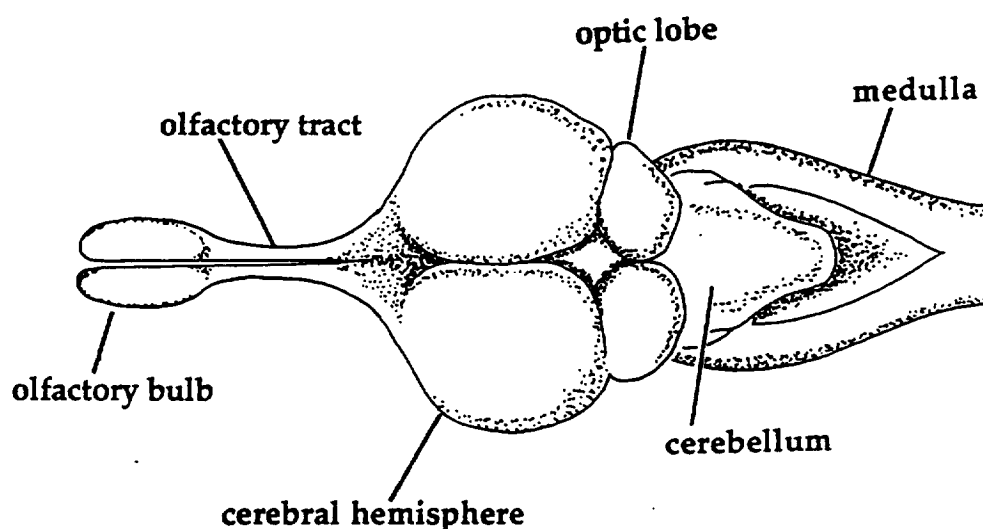
Figure 2. Dorsal view of the brain of *Alligator*. Modified from Romer and Parsons (1977).

Extinct reptiles. -- Retrieval of information about the structure of the nervous system of extinct reptiles is possible through study of the bony cavities that enclosed it in life. Peripheral nerves travel predominantly in the soft tissues, and therefore few records of them remain. However, the central nervous system is protected and supported by the braincase and vertebral column. Endocranial casts of the braincase may be naturally formed by sediment infilling or secondarily made by cleaning the internal

surfaces of the braincase and then preparing rubber molds. Hopson (1979) estimated that only about one half of the endocranial space of reptiles is actually filled by the brain, meaning that endocranial casts can give only a rough idea of the size and proportions of the brain.

Each bone of the reptilian vertebral column houses a segment of the spinal cord in life. The size (cross-section) of the spinal cord at a given segmental level is reflected quite accurately by the size of the neural canal of the vertebra of the same segmental number (Fig. 3). Measurements of cross-sectional area of the neural canal in each vertebra therefore reflect the changing size of the spinal cord throughout its length, and allow prediction of the location of limb-level plexuses (Fig. 4).

PREDICTING THE LIFESTYLES OF DINOSAURS

Intelligence. -- A general argument may be made that the larger the brain size relative to body size, the greater the areas of the brain dedicated to integration functions. It is these integration functions that allow behavioral flexibility, a trait generally equated with "intelligence".

The relationship of brain size to body size in living reptiles has been documented by many workers, most thoroughly by Crile and Quiring (1940). Jerison (1973) plotted brain size versus body size for many vertebrates, demonstrating that brain size increases with, although not as quickly as, body size. His graphs also show that mammals have markedly larger brains than do reptiles of the same body size (Fig 5).

Extrapolation from the trends shown by recent reptiles allows evaluation of the relative size of dinosaur brains, but also requires estimates of both brain mass and body mass in the extinct taxa. Estimates of dinosaur brain volume may be calculated by water displacement of natural or artificial endocasts. Volume is converted to mass in a 1:1 ratio, because vertebrate tissue has approximately the density of water. Estimation of dinosaur body mass is more problematical. The typical method is to measure the water displacement of a model of known scale and then to multiply the volume displaced by the cube of the linear relationship between model and dinosaur. Again, the volume obtained by this method may be converted to mass because of the relationship stated above (Alexander, 1989). Masses calculated vary somewhat with the model used.

As is evident from the graph (Fig. 5), dinosaur brains are, as a group, of the size one would expect in very large reptiles -- they fall on and around an extension of the line that documents brain/body relationships in living reptiles. We may therefore predict that dinosaurs had behavioral flexibility, or "intelligence", rather similar to that of modern reptiles.
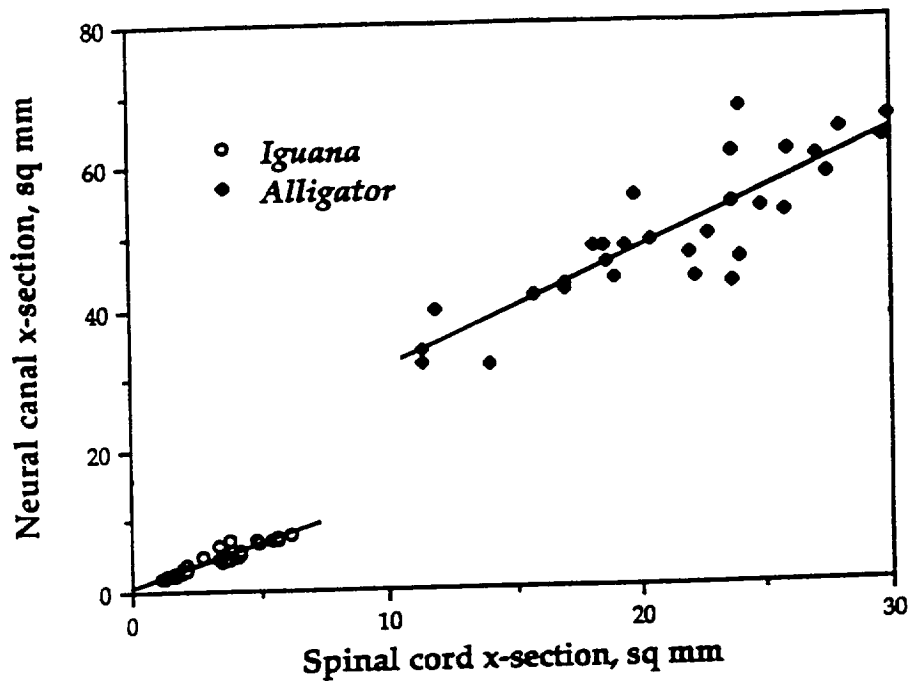
Figure 3. Relationship between the size of the spinal cord and the size of the neural canal in *Iguana* and *Alligator*. For *Iguana*, y = 0.55 + 1.2x, r=0.95; for *Alligator*, y = 15.33 + 1.62x, r= 0.86.
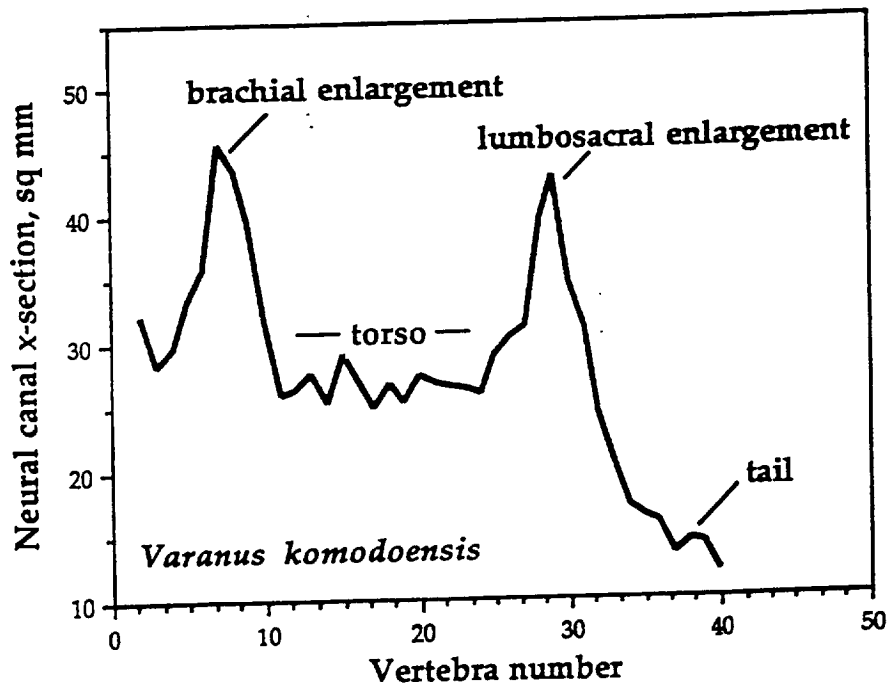
Figure 4. Size of the neural canal by segment in the komodo dragon, *Varanus komodoensis*.

Hopson (1977) looked at the variation in relative brain size *between* different groups of dinosaurs. He found that carnivorous and bipedal dinosaurs consistently had larger relative brains than herbivorous and quadrupedal taxa. Small, carnivorous, bipedal dinosaurs rivaled birds in relative brain size, and are in fact probable close relatives.
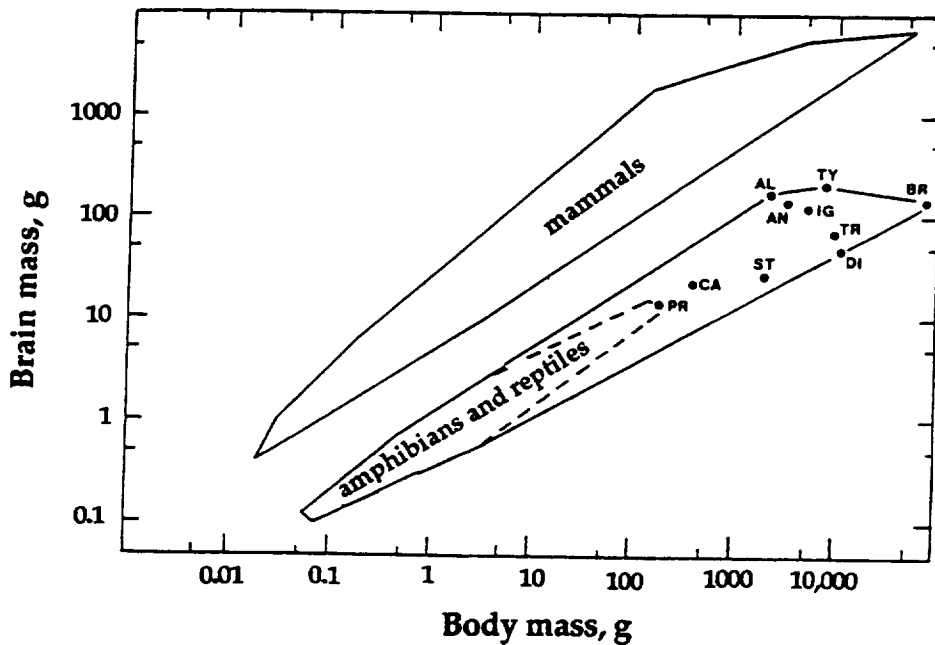
Figure 5. Relationship between body size and brain size in dinosaurs superimposed on grouped data for living amphibians, reptiles and mammals. Dinosaurs: AL, *Allosaurus*; AN, *Anatosaurus*; BR, *Brachiosaurus*; CA, *Camptosaurus*; DI, *Diplodocus*; IG, *Iguanodon*; PR, *Protoceratops*; ST, *Stegosaurus*; TR, *Triceratops*; TY, *Tyrannosaurus*. Modified from Hopson, 1979.

Perhaps this is the place to contradict the often-repeated contention in the popular literature that *Stegosaurus* had a brain "the size of a walnut". The most completely described *Stegosaurus* endocast (USNM 4936) is a composite based on several specimens (Hopson, 1979). Although *Stegosaurus* apparently had a relatively smaller brain than many other dinosaurs, the dimensions of this specimen (approximately 17cm x 3 cm x 3cm) are surely much larger than, and not at all the shape of, a walnut.

Sensory modalities. -- The ability to predict sensory modalities used by various dinosaurs on the basis of brain anatomy is restricted by the fact that reptile brains do not fill the braincase entirely. As a result, the details of brain structure are only rarely modeled on the inside of the skull bones. Hopson (1979) compared brains and endocasts from the same specimens of the crocodilian *Caiman*, and found that brain anatomy is more faithfully

reflected by the braincase in juvenile than in adult specimens. He also found that the anatomy of the forebrain was considerably better preserved than that of the medulla, in large part because of the presence of circulatory sinuses between the medulla and braincase.

With these restrictions in mind, it is possible to compare endocasts of members of different dinosaur subgroups, evaluating the relative importance of brain areas receiving and processing information from different sense organs. Dorsal views of endocranial casts of the small troodontid theropod *Stenonychosaurus* (a carnivorous saurischian) and of the pachycephalosaur *Pachycephalosaurus* (a herbivorous ornithischian) are presented in Fig. 6, and demonstrate the type of inferences that may be drawn from endocasts. A comparison of the two specimens shows that the *Pachycephalosaurus* brain had much larger olfactory lobes, suggesting that the sense of smell played a much larger role in its sensory input than it did in the theropod. Conversely, the *Stenonychosaurus* endocast has a relatively larger cerebellum and large cerebral hemispheres, suggesting the more important role of muscular coordination and behavioral flexibility in its lifestyle than in that of the herbivore.

Figure 6. Endocranial casts of A, *Pachycephalosaurus* (modified from Giffin, 1989) and of B, *Stenonychosaurus* (modified from Hopson, 1979) reproduced to same size for comparison. cbl, cerebellum; cer, cerebrum; d ls, diverticulum of lateral circulator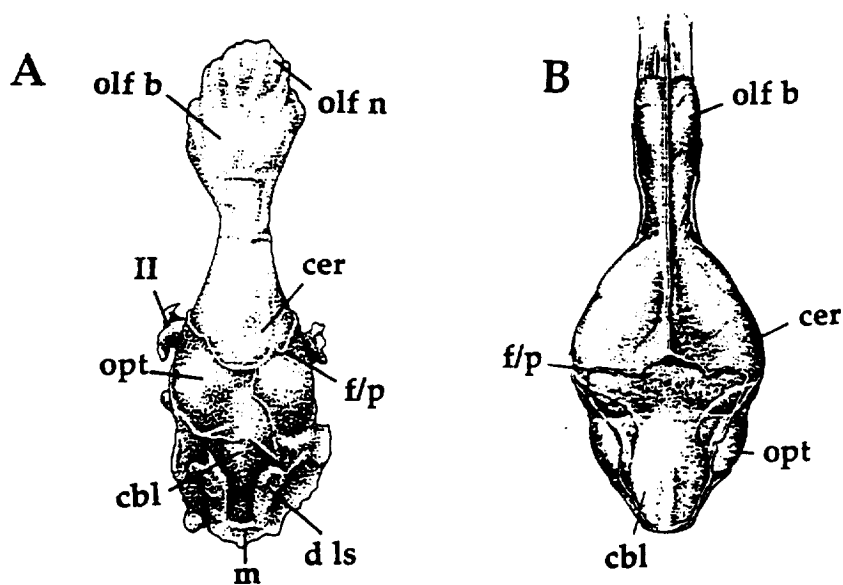y sinus; f/p, frontal/parietal suture; m, medulla; olf b, olfactory bulb; olf n, olfactory nerve; opt, optic lobe; II, second cranial (optic) nerve.

Endosacral enlargements. -- As mentioned above, variation in the size of the neural canal has been shown to reflect size of the enclosed spinal cord in living birds, crocodilians and lizards. It has been a source of interest, and some amusement, therefore, that the neural canal of the sacral vertebrae of stegosaur and sauropod dinosaurs is massively enlarged, rivaling or exceeding the size of the brain case. O. C. Marsh (1881) referred to the enlarged endosacrum of *Stegosaurus* as a "posterior brain case", initiating decades of comments about the possibility of a second brain finally put to rest by T. Edinger (1961).

Since we may be reasonably sure that no second brain existed, what other explanations are available to account for the enlarged endosacra? Although only distantly related taxonomically, both stegosaurs and sauropods were graviportal herbivores with large tails. One possibility is that an enlarged sacral spinal cord innervated an especially powerful and flexible tail. This hypothesis may be evaluated by an examination of the nervous supply to the caudofemoralis muscle, the major effector of lateral tail movement in living lepidosaurian and crocodilian reptiles (Rewcastle, 1981), and almost surely present in the same role in dinosaurs (Gatesy, 1990). Caudofemoralis innervation in the living relatives of dinosaurs is very consistently located at the posterior end of the lumbosacral plexus, from nerves that exit between the posterior sacral and anterior caudal vertebrae. The plexus itself is also very uniform throughout diapsids, and its position relative to the vertebrae of the dinosaur sacrum can be predicted (Fig. 7) by a comparison with living taxa. However, this location does NOT correspond with that of the maximum endosacral enlargements in dinosaurs, which lie some three segments anteriorly, in the area of nerves supplying the hind limbs (Giffin, 1991). This observation seriously challenges the contention that a large and flexible tail is responsible for dinosaur endosacral enlargements.

Is it then reasonable to predict that the enlarged stegosaur and sauropod endosacra reflect enhanced neural supply to the hind limbs, which supported much of the weight of these graviportal giants? This hypothesis may also be tested, by a comparative examination of relative size of the lumbosacral enlargement in living reptiles and birds with different hind limb use. Using the cross-sectional area of the spinal cord in the torso as a standard, the relative size of the lumbosacral enlargements in animals of different body size and limb use may be directly compared. Sprawling reptiles that use both the torso and the limbs in locomotion have relatively small enlargements; the spinal cord at limb levels is typically less than twice the size of that in the torso. Limb-walking lizards, such as *Chamaeleo*, use the limbs almost exclusive of the torso, and show slightly enhanced hindlimb enlargements. Birds are bipeds with rigid torsos, and have lumbosacral spinal values up to three times as large as those of the torso. These values are independent of the size of the animal, and agree generally with those observed for many
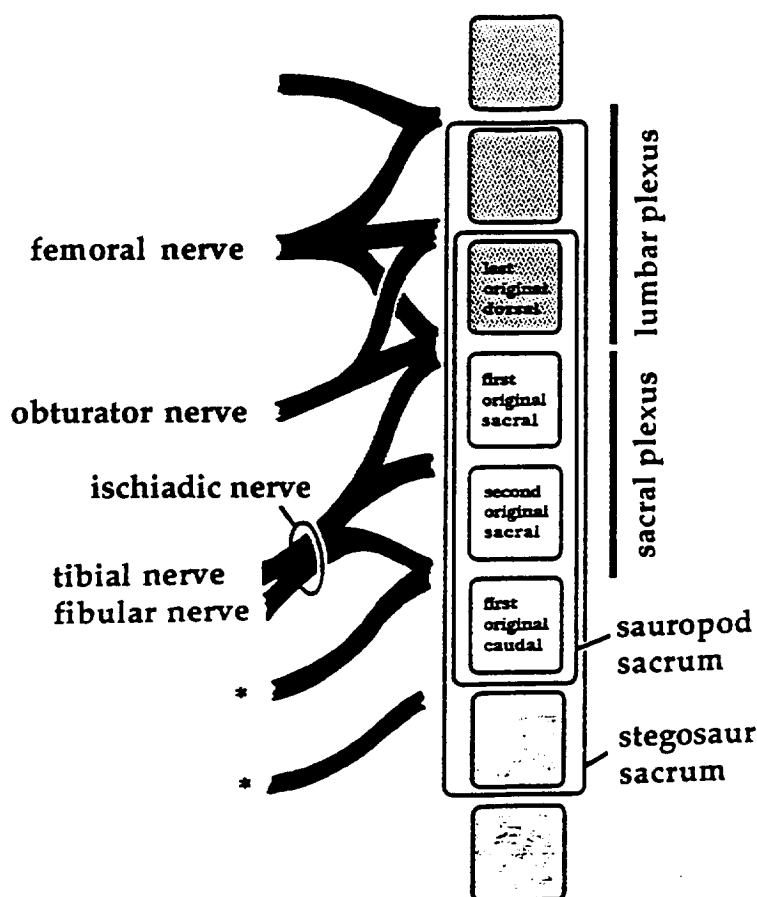
Figure 7. Reconstruction of the lumbosacral plexus of dinosaurs, with segmental positions of the sacra of stegosaurs and sauropods indicated. Caudofemoralis innervation arises from the most posterior segments of the plexus. Modified from Giffin (1991).

dinosaur taxa (Ceratopsia, Ornithopoda, Theropoda; Giffin, 1990). However, the endosacral enlargements of stegosaurs (4 - 7 times the torso measurements) and sauropods (11-15 times the torso measurements) far exceed these values. The osteological observations that suggest that stegosaurs and sauropods were rather slow, graviportal quadrupeds do not support a hypothesis of neural supply to the hind limbs that far exceeds that of related taxa.

A final hypothesis suggests that in addition to the spinal cord, some dinosaur endosacra housed avian-style glycogen bodies. All birds possess a glycogen storing organ between the dorsal funiculi of the sacral spinal cord. The function of the organ is not confidently known, but it may play a role in synthesis of lipids used by the central nervous system (De Gennaro, 1982). As a result of its presence, the neural canal of birds may be twice as large as the spinal cord at lumbosacral levels that correspond to the location of the enlarged endosacra of dinosaurs. Although not proven, the hypothesis of

glycogen body presence in at least some dinosaur groups is consistent with the size and location of the glycogen body of birds. It is further supported by the phylogenetic relationship of birds and dinosaurs, and provides a more satisfactory explanation of dinosaurian anatomy than do hypotheses of neural supply to the tail or hind limbs.

Forelimb use. -- What did *Tyrannosaurus rex* do with its tiny arms? Some authors have suggested that despite small relative size, the forelimbs of *T. rex* had utilitarian functions such as food manipulation, sexual grappling, or propping during rising from a prone position (Molnar and Farlow, 1990). Because neural supply to a limb reflects not only limb size but also density of innervation and thus limb use, it may be used to test the hypothesis that *Tyrannosaurus* forelimbs had a biologically significant use not apparent from their size.

Large flightless birds (ratites) may be used as a means of evaluating the extent of neural supply to limbs of different relative size and use in a taxon closely related to dinosaurs (Giffin, in press b). Relative forelimb size in ratites may be estimated by summing the length of forelimb elements and dividing by femur circumference, a common estimator of body mass in birds (Anderson et al., 1985). Among living ratites, ostriches and rheas use their relatively large wings, which possess 3-digit hands, as aids in locomotion and courtship. Cassowaries, emus and kiwis have much smaller relative wing size, a one-digit hand, and no observed wing use. Tinamous are weakly flighted ratite relatives, while the extinct moas had no wings at all. As might be expected (Fig. 8) the relative size of the brachial enlargement of the neural canal is largest in those taxa with the largest relative wing size and the most extensive wing use. However, even the moas show a small limb level enlargement of the neural canal, perhaps reflecting neural supply to the pectoral girdle.

Relative forelimb size and extent of forelimb innervation in the theropod genera *Carnotaurus, Saurornitholestes, Deinonychus, Dilophosaurus* and *Allosaurus* fall within the range established for ratites, moas, and tinamous. Dinosaurs with limb anatomy suggestive of manipulative use (*Deinonychus, Allosaurus, Saurornitholestes, Dilophosaurus*) vary in relative size of brachial enlargements, but in every case the brachial neural canal is at least twice that of the torso. *Carnotaurus* and *Tyrannosaurus* have brachial enlargements that are similar in size to those of ratites with no observed use of the forelimb and to those of the wingless moas. The rather disappointing conclusion is that, as their relative size suggests, the forelimbs of these giant theropods had no significant biological function.

In summary, the range of questions that may be asked about dinosaurs is broader than previously recognized. Bones of extinct vertebrates contain
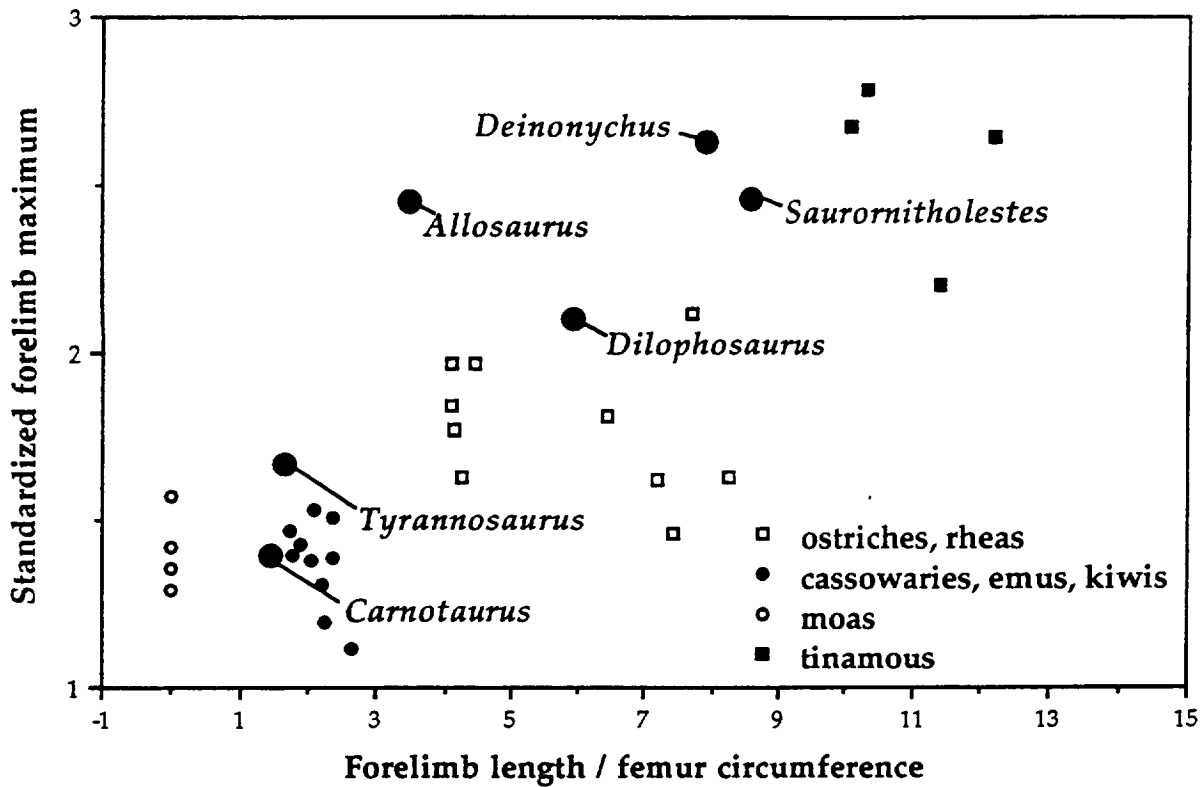
Figure 8. Size of the maximum brachial enlargement of ratites and dinosaurs of different relative forelimb and body size.

clues to soft tissue systems that may be powerful indicators of lifestyles and behaviors once assumed to be beyond our ability to recover. Among these systems the nervous system is unique because of its roles in the sensing and the processing of information received from the environment, and in the control of responses to the environment.

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Thermal Physiology of the Dinosauria:
Evidence from Oxygen Isotopes in Bone Phosphate

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INTRODUCTION

Dinosaurs were an abundant group of reptiles that originated in the mid-Triassic. They rapidly diversified, filling all of the ecological niches for large-bodied terrestrial vertebrates by the Late Triassic and dominated this landscape for 163 m.y. Yet due to the lack of direct evidence little is known about their metabolism. The question as to whether dinosaurs were "warm-blooded" or "cold-blooded" has been debated for over 25 years. Knowledge of dinosaur thermal physiology is critical if we are to understand how they lived and functioned. This knowledge can then be used to help answer questions regarding to their origin, diversification, and their eventual extinction. The question that is being resolved here is, "How do you stick a thermometer into dinosaur bone?".

Thermal Physiology.-- The terms "warm-blooded" and "cold-blooded" are not entirely accurate in describing the possible physiological mechanisms behind the thermoregulation of animals. **Endothermy (warm-bloodedness) is a pattern of** thermoregulation in which body temperature depends upon a high and controlled rate of metabolic heat production (Bligh and Johnson, 1973), whereas in **ectothermy** (cold-bloodedness), body temperature is dependent upon regulated uptake of heat from the environment. These patterns of thermoregulation are simply end members along a continuum of physiologic strategies. **Homeothermy** is maintenance of body temperatures within $\pm 2^{\circ}C$ despite much larger cyclic daily or seasonal variations in external ambient temperature. **Heterothermy** describes body temperatures that regularly fluctuate well beyond these limits. For example, both mammals and birds are endothermic homeotherms which depend upon constant, high metabolic heat production, muscular shivering, and insulation (fat and hair or feathers) to maintain high constant body temperatures. Modern reptiles, however, do not possess the highly sophisticated mechanisms for long-term high rates of internal heat production, nor do they have effective insulation. Their body temperatures are not maintained within $\pm 2^{\circ}C$ either. daily or seasonally and thus are defined as ectothermic heterotherms. Reptiles may, however, exert considerable control over their body temperatures and many are capable of maintaining body temperatures above the surrounding environment through the use of behavioral adaptations (Greenberg, 1980).   Reptiles, like all vertebrates, incorporate metabolic heat production within their thermoregulatory strategy; however, this is not their main source of heat uptake nor is it enough to maintain high body temperatures.

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How does an animal's thermal physiology affect how it lives? Endothermy and
ectothermy are simply two different strategies toward achieving a common goal,
maximum individual reproduction. This results in contrasting life histories. In order to
support high rates of metabolism and maintain a constant body temperature,
endotherms must eat large amounts of food. Thus, the costs of maintaining endothermy
are high. Ectotherms, on the other hand, can take advantage of a plentiful food supply,
but can also survive much longer periods of scarce resources by further reducing their
metabolism. The lower maintenance costs of an ectotherm's low metabolism allows
them to route a higher percentage of their energy intake toward growth and
reproduction. Growth in ectotherms, though more efficient, is episodic (resulting in
growth rings within bones) and thus much slower than for endotherms. Juvenile
endotherms are capable of maintaining relatively constant and rapid rates of growth.
Endotherms reach adulthood (i.e., sexual maturity) much more rapidly than similarly
sized ectotherms. However, this faster pace of life results in shorter periods of
reproductive potential and shorter lifetimes for endotherms. A high metabolic rate also
allows terrestrial endotherms to be active under a much greater range of environmental
conditions than ectotherms. It has been argued by Bennett and Ruben (1979) that the
evolution of endothermy was the product of evolutionary pressures for increased
aerobic capacity. Endotherms do have a much greater aerobic capacity than ectotherms
which gives them the stamina to be physically active for prolonged periods of time.
They are able to more rapidly repay oxygen debts generated during anaerobic exertion
which allows them to recover much faster from periods of strenuous exertion.
Understanding the thermal physiology of the dinosauria, therefore, is very important for
deciphering their life histories.

Previous Thought on Dinosaur Physiology.-- In the absence of direct means of
measuring dinosaur body temperatures and their fluctuations, previous studies have had
to focus on indirect evidence. The case for endothermy has been championed by
Bakker (1986). The main argument centers around the fact that mammals are presently
dominant over reptiles in all of the large body size terrestrial niches, even in tropical
climates where reptiles should supposedly be capable of achieving homeothermy
without the expense of high metabolism. Dinosaurs and mammals evolved at about the
same time, and it was the progenitors of the mammals (the therapsids) which actually
dominated the Triassic terrestrial assemblages before the dinosaurs. If mammals were
endothermic and dinosaurs were not, then it should have been the mammals that
radiated at the expense of the dinosaurs in the mid to late Triassic. Hence, Bakker's
conviction that because the dinosaurs radiated to all of the large size classes they must
also have been endotherms. Alternatively, Benton (1983, 1986) suggested that the
dinosaurs benefited from several mass extinctions near the end of the Triassic and thus
did not outcompete mammals, but radiated rapidly into open ecospace or an adaptive
landscape from which they later could not be displaced. Dinosaurs were characterized
by an erect posture and many walked bipedally. Other than dinosaurs, only birds and
mammals have a similar posture and gait. As mammals and birds are endothermic, it
has been postulated that dinosaurs should also be endothermic (Bakker, 1986; Ostrom,
1980) based upon their posture and gait. Alternative arguments imply that endothermy
need not be associated with upright posture but that upright posture is simply a
necessity for attaining large size (Norman, 1984). The relatively small brain size of
most dinosaurs (Feduccia, 1974) has been used as evidence that dinosaurs could not
have maintained endothermy. Hopson (1980), though, has found that small theropods
and ornithopods do have brain sizes within the range of birds and mammals, indicating
that these small dinosaurs (based on this evidence) may have been capable of
endothermy. Supposed high activity levels of certain dinosaurs such as *Deinonychus*

(Bakker, 1986) and group activity as evidenced from trackways (e.g., Bird, 1944) and bone beds of ceratopsian herds (Philip J. Currie, personal communication, 1990) are also indicative of mammal or birdlike behavior. However, it is not outside the possibility that relatively complex, gregarious behavior lies within the behavioral realm of heterotherms. For example, crocodiles show some degree of parental care (Pooley and Gans, 1976) where mother crocodiles hear the cries of the new hatchlings and proceed to collect them in their mouths and carry them to the relative safety of the water.

The distribution of dinosaurs at mid to high latitudes (Alaska and Antarctica; Weishampel, 1990) has been used as evidence of dinosaurian endothermy (Bakker, 1975) and this evidence is strengthened as it now appears (Sloan and Barron, 1990) that Mesozoic continental climates in these regions were not as equable (warm) as previously thought (e.g., Dorf, 1970). Sloan and Barron's (1990) climatic models indicate that continental interiors reached freezing levels on a seasonal basis. Alaskan dinosaurs have been postulated to have undergone long migrations in order to have avoided seasonal extremes (Parrish et al., 1987). However, recent evidence (Gasparini et al., 1987; Tom Rich, personal communication, 1993) of Antarctic dinosaurs strengthens support for endothermy unless previous paleogeographic reconstructions of Antarctica over the South Pole can be shown to be incorrect. Bakker (1980, 1986) has presented evidence that the low predator/prey ratios of dinosaurs are more similar to those of large mammals than to the high predator/prey ratios of reptiles (both modern and fossil). However, this evidence is equivocal (Farlow, 1980, 1990) due to the overprint of taphonomic vagaries and the unknown relationships of Mesozoic food webs which complicate such analyses. Evidence from bone histology (Ricqles, 1974) indicates rapid growth rates in dinosaurs and an internal structure more similar to mammals than reptiles: absence of growth lines indicates continuous, noncyclical growth. However, this mode of growth may also be developed with mass homeothermy and may only be a necessity for the structural adaptation to the stresses provided by large body sizes (Ricqles, 1980). Dinosaur bone is not invariably mammal-like and may have both mammalian and reptilian characteristics (Reid, 1985). Though many dinosaur bones do show fibrolamellar bone indicative of rapid growth, Reid (1985) showed that some dinosaurs (e.g., *Iguanodon* and *Rhabdodon*) have growth rings and that some known ectotherms from the fossil record have some fibrolamellar bone. Thus, while fibrolamellar bone suggests physiological differences between dinosaurs and modern reptiles, it does not necessarily imply endothermy. The final indirect argument for dinosaur endothermy states that birds are endothermic and uses evidence that birds directly evolved from small theropods (Gauthier, 1988). Therefore, at least these dinosaurs are implied to be endotherms. However, some avian biologists (Martin, 1980, 1983) do not believe that birds are dinosaurian descendants but that they diverged from Triassic archosaurs at the same time that dinosaurs were also evolving.

Cases against dinosaurian endothermy similarly involve indirect evidence. It has been suggested that large sauropods do not have the feeding apparatus capable of supplying enough food to sustain endothermy, though the discovery of sauropod gizzard stones have shown that they could have processed large quantities of food (Bakker, 1986). It has been hypothesized that the constantly equable climates of the Mesozoic allowed dinosaurs of large size to maintain high homeothermic body temperatures without elevated metabolic rates (Colbert, 1951; Spotila et al., 1973; Ostrom, 1980; Hotton, 1980). However, the equability of Mesozoic continental paleoclimates has recently been challenged (Sloan and Barron, 1990). Dinosaurs must also pass through small body sizes on their way to adulthood, and juvenile dinosaurs would not have the advantages of mass homeothermy. Spotila et al. (1973) suggest that animals longer

than 1 m are capable of maintaining core temperatures above ambient temperature for long periods. However animals of this size must do so through countercurrent heat exchange which rapidly cools the limbs toward ambient temperature. Keeping body temperatures above ambient does not necessarily mean that homeothermy is maintained over seasonal changes in temperature. Finally, many authors (e.g., Cloudsley-Thompson and Butt, 1977; Spotila, 1980) believe that large, endothermic dinosaurs would not have been able to dissipate their own metabolically produced heat due to their large mass/surface area ratio and would have overheated. However, perhaps dinosaurs were capable of storing heat from daytime as do camels, raising body temperatures above normal to have it dissipated each night without damaging tissues or enzyme functions. Evidence of Pleistocene elephants and Miocene rhinoceroses (e.g., *Mammuthus* and *Indricotherium*) which reached shoulder heights of 4.5 m and weights of 11- 20 tons also suggests either that endothermy is possible at these large sizes or that these mammals were not endotherms but rather mass homeotherms.

OXYGEN ISOTOPES

Oxygen is one of the most abundant elements in the earth's crust, atmosphere, and hydrosphere as well as in animal blood, tissue and bone. Atoms of oxygen may contain between 16 and 18 neutrons in their nucleus though the number of protons remains constant. The differences in the mass of these "isotopes" of oxygen result in their having slightly different physiochemical properties. These differences in the chemical properties can lead to isotope effects in chemical reactions. One of the most useful of these mass related isotope effects is the dependence upon temperature of the oxygen isotope exchange between fluid and mineral phases. What this means is that during the formation of bone, the ratio of the oxygen-18 to oxygen-16 ($^{18}O/^{16}O$) atoms in the bone phosphate [$Ca_{10}(PO_4)_6(OH)_2$]will vary depending upon: a) body temperature and b) the $^{18}O/^{16}O$ value of the body water with which the oxygen atoms of the bones are exchanging. Therefore, if one knows the isotopic composition of both the bone phosphate and the body water, it is possible to calculate the body temperature at which the bone was formed.

An equation correlating temperature with phosphate and water oxygen isotopes was derived by Longinelli and Nuti (1973) and has been applied successfully on modern mammals (Luz and Kolodny, 1989). Body water composition depends upon the $^{18}O/^{16}O$ value of ingested water as well as on the rate of metabolism. Without knowing the body water $^{18}O/^{16}O$ values for different dinosaur species, it is not possible to calculate individual body temperatures. All that remains of the dinosaurs are the bones. However, body water isotopic composition is in equilibrium throughout every individual (Pflug et al., 1979; Wong et al., 1988; Schoeller, 1986). Thus the body water, from which all oxygen atoms in the bones of any given individual are exchanging, contain essentially identical $^{18}O/^{16}O$ values. Any variation in the $^{18}O/^{16}O$ values from different bones within any individual should correlate to differences in the temperature at which those bones were formed. This means that the $^{18}O/^{16}O$ values of the bone phosphate from all skeletal elements within an individual endotherm should have very little variation. Modern reptiles, however, do not maintain constant temperatures throughout all body regions (Cloudsley-Thompson, 1971; Templeton, 1970). McNab and Auffenberg (1976) reported up to 14°C daily fluctuations in the body temperature of Komodo dragons. Seasonal temperature fluctuations are recorded by the variability of the oxygen isotopic compositions in the bones.

APPLICATION OF ISOTOPES TO DINOSAUR PHYSIOLOGY

There are two ways of assessing oxygen isotopic variation within an animal: intrabone variation and interbone variation. Multiple samples taken across a bone serve as time series of temperature and/or body water $^{18}O/^{16}O$ variability during the growth of that bone. This pattern of isotopic variability, however, is modified by processes of bone remodeling (the resorption and reprecipitation of bone for maintaining its mechanical and physiological competence). Therefore, the variation across a bone cannot be cyclically correlated to specific daily, seasonal or annual variations in body temperature or body water $^{18}O/^{16}O$ values as can be done for example with bivalve shells. Remodeling rates in human bone vary between 2 and 10% per year depending on the bone type and the skeletal element (Francillon-Vieillot et al., 1990). These rates of bone turnover are longer than the monthly or seasonal sources of isotopic variability occurring within an individual. Thus, seasonal isotopic variability will appear in the isotopic composition of the bone phosphate but the pattern of variability will be dependent upon the pattern of bone remodeling.

Each difference of 1 part per thousand (‰) in the $^{18}O/^{16}O$ ratio of the bone phosphate between samples within a skeletal element is the result of a 4.3°C difference in temperature between the times of bone formation. This is calculated using the slope of the phosphate-water temperature equation (Longinelli and Nuti, 1973). Positive isotopic values (more ^{18}O) reflect colder temperatures and negative isotopic values (more ^{16}O) reflect warmer temperatures. An endotherm, therefore, should have temperature related isotopic variability of less than 1‰ in any bone. An ectotherm on the other hand, will have greater than 1‰ variability in its bones. The amount of temperature related variability in an ectotherm will depend somewhat upon its size and the magnitude of the seasonal climate changes over which it is actively growing or remodeling bone. In ectotherms, the amount of intrabone isotopic variability will also change between skeletal elements. All animals lose heat more rapidly from their extremities (limbs and tail) than from the central core or trunk of the body. This is due to the relatively small mass/surface area ratio in the extremities. For ectotherms in the size range of most dinosaurs, this means that the extremities will undergo much greater temperature fluctuations in the extremities than in the trunk of the body where the greater mass helps retain heat. Therefore, intrabone isotopic variability should increase in bones from proximal to the distal extremities. Endotherms, however, should have similar or only slightly increased isotopic variability from the limbs and tails than do bones from the central trunk (i.e., ribs and dorsal vertebrae). Interbone isotopic variability will similarly relate to thermal physiology. In most cases, the extremities will, on average, be colder in ectotherms than the core of the body. This again, is due to more rapid heat loss from the extremities, and the less efficient blood circulation of ectotherms. In colder conditions this effect may be magnified by countercurrent heat exchange mechanisms which are used to help retain heat within the body core while allowing the extremities to fall toward ambient temperatures. Terrestrial mammals and birds will also use heat exchange although there is often increased insulation (hair or feathers) along the extremities to reduce the temperature extremes experienced by the limbs.

When interpreting the isotopic variability in extinct vertebrates, both intrabone and interbone components are used. Ectotherms will have greater than 1‰ intrabone

variability within all skeletal elements with increasing variability in bones of the extremities. They will also have mean isotopic values in the extremities which are much more positive (colder) than in the ribs and dorsal vertebrae. Endotherms will have intrabone variability less than 1‰ in all skeletal elements and the mean values from the extremities will be similar to, or only slightly more positive (<1‰) than those of the ribs and dorsal vertebrae. What about mass homeothermy? Metabolic rates for all animals scale with increases in body size. Extremely large dinosaurs will have very low mass specific metabolic rates because of their size. In environments where there is little seasonal change in temperatures, such large dinosaurs as the sauropods should have been able to maintain homeothermy both in the body core and the extremities by virtue of their great mass (Spotila et al., 1991). They would be indistinguishable from endotherms with low intra- and interbone isotopic variability. However, if seasonality was relatively large, these dinosaurs may still have been able to maintain homeothermy in the core body though the extremities should then have experienced heterothermic conditions. In this situation, dorsal vertebrae and ribs would have low intrabone isotopic variability while bones in the extremities would have increased isotopic variability. Interbone isotopic variability could also be low due to temperatures in the extremities fluctuating around the temperature in the core body as a result of heat dumping in warmer periods and heat retention in colder periods. The most accurate method of determining the thermal physiology of large dinosaurs is to analyze juveniles to determine if they maintained homeothermy as they grew and compare the results with adult isotopic variability. The possibility exists that the larger dinosaurs were either: 1) endotherms throughout their life history, 2) endotherms as juveniles and mass homeotherms as adults, or 3) ectotherms as juveniles growing into mass homeotherms as adults.

RESULTS AND DISCUSSION

Several Late Cretaceous and Late Jurassic dinosaurs have been analyzed for intrabone isotopic variability (Figure 1 A, B,C). The total range of isotopic variability of bones from the body core (ribs, dorsal vertebrae, pelvic girdle) in the Cretaceous dinosaurs remain well below 1‰, indicating that all of the bones were formed under homeothermic conditions ($\pm 2^{\circ}$C). The pelvic girdles of the Jurassic dinosaurs have intrabone variations suggesting a heterothermic temperature range (± 2.2 to 2.8°C). Intrabone variability within the extremities of all of the Cretaceous dinosaur specimens fall within the range of homeothermy. The femur of *Ceratosaurus* and the tail of *Allosaurus* slightly exceed 1‰. There are no trends in the intrabone isotopic variability between the bones from the body core and the extremities suggestive of ectothermy or mass homeothermy. The slightly >1‰ range found in the few bones of the Jurassic specimens are not much different from the rest of the bones just below the 1‰ range. This trend suggests that the isotopic variability may be due to seasonal change in the isotopic composition of ingested waters in these animals rather than shifts in body temperature.

It is easiest to see the effect of interbone variability by examining the temperature differences which would be responsible for the variability if it were the sole factor (Figure 2). Simply subtracting the most negative isotopic value from the most positive

A   ▥ **Ribs**   ■ **Dorsal vertebrae**   ▨ **Pelvic girdle**

B   ▥ **Upper leg**   ■ **Lower leg**   ▨ **Feet**
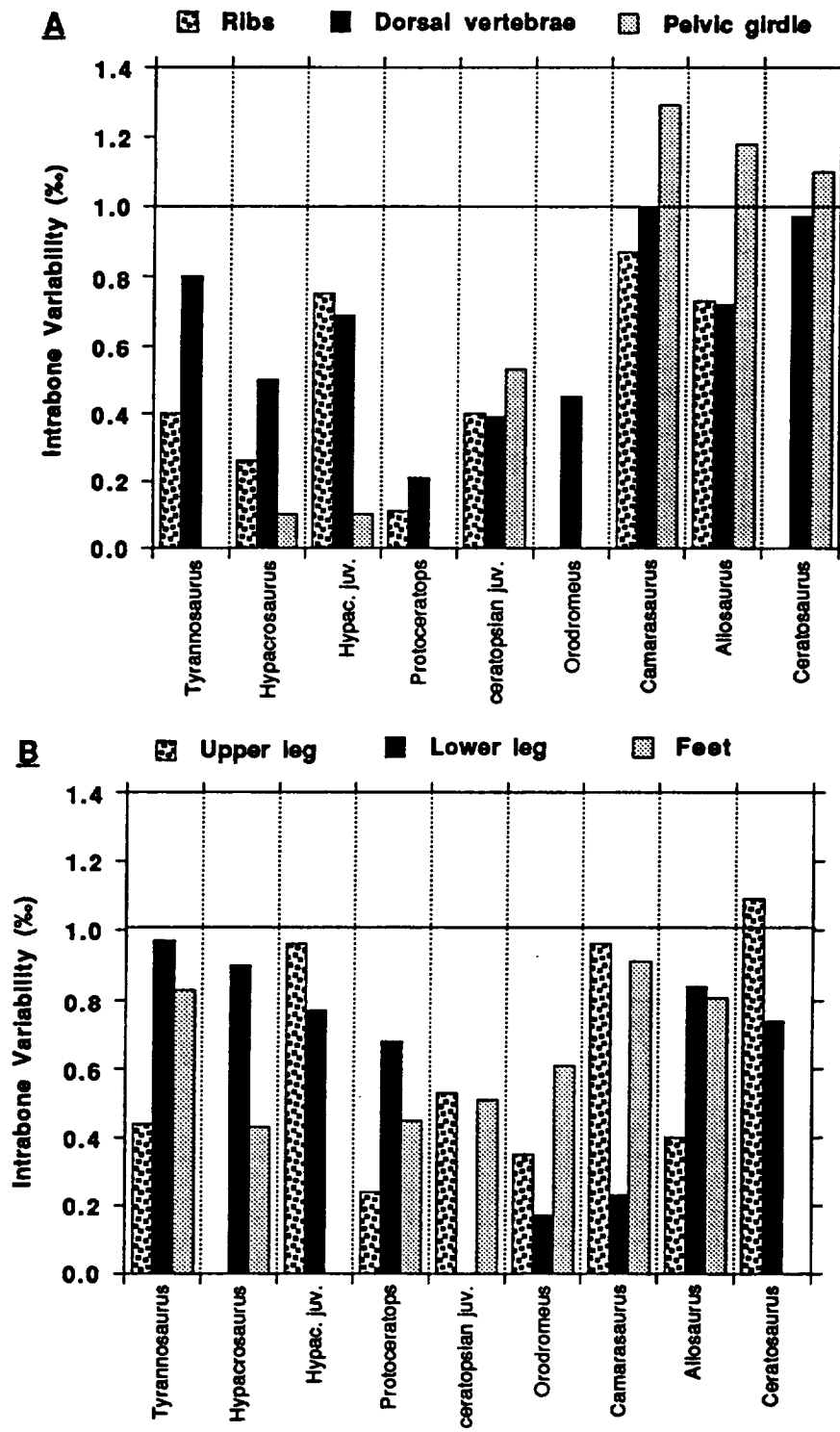
Figure 1 description overleaf
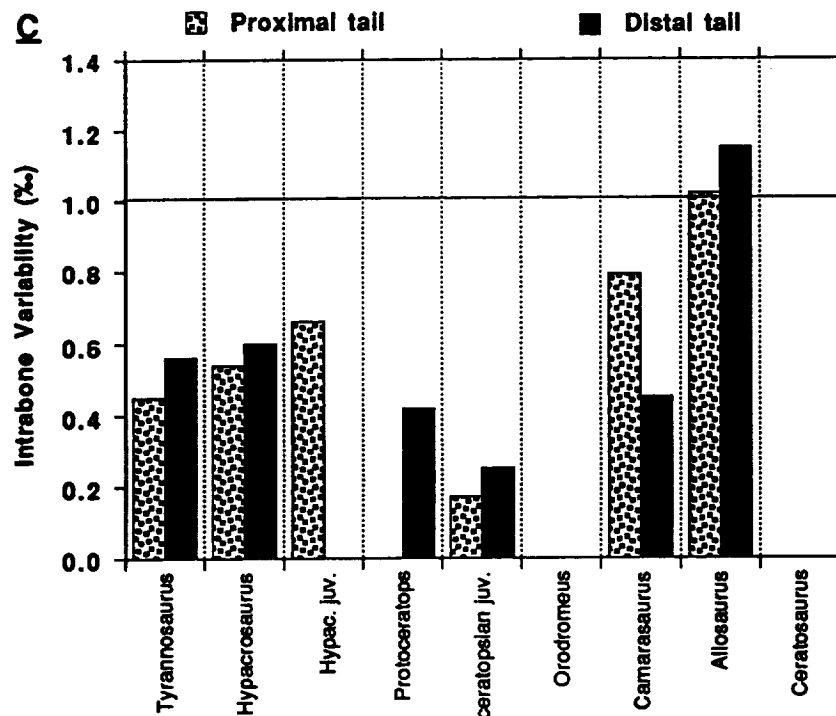
FIGURE 1--Maximum intrabone isotopic variability for skeletal elements within the; A) core body, B) legs, and C) tail for each of the dinosaurs studied. Variability does not consistently increase from the core through the extremities.

value and multiplying by the slope of the phosphatetemperature equation (4.3) will give you the maximum possible temperature difference for any given animal. For most of the dinosaurs, this temperature range would put them outside the limits of homeothermy. However, this is also the case with most modern endotherms and ectotherms. This anomaly is due to seasonal changes in the isotopic values of ingested water. These changes in water isotopic values may result from migration or seasonal changes in aridity or temperature. The pattern of bone remodeling is also a factor. Therefore, when analyzing interbone variation, it is best to use the average isotopic value for each bone. Differences in the average isotopic value between skeletal elements most likely represents actual differences in the temperature during bone formation between the different body regions. By using the skeletal element with most negative average isotopic value (which always comes from the warmer body core) and the one with the most positive average isotopic value (coldest temperature within the extremities) it is possible to get a more realistic look at the temperature difference between the body core and the extremities. When this is done, all of the dinosaurs appear to be homeotherms with close to or less than a 4°C total range in body temperature.

The Cretaceous dinosaurs range in size from 1.5 m and ~60 to the ~6000 kg (Horner, 1993)*Tyrannosaurus* (similar to a bull African elephant). All are from Montana which was located at 53°N latitude. However, the climate in Montana at that time was similar to present day Louisiana or North Carolina. The seasonal temperature changes may not
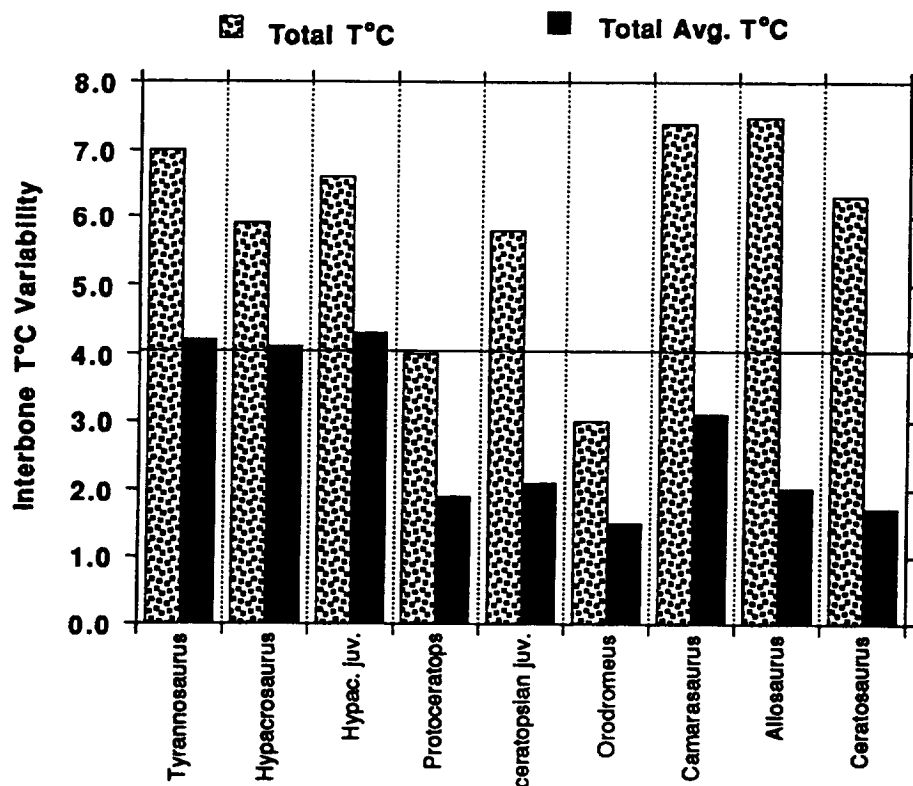
FIGURE 2-- Conversion of interbone isotopic variability into temperature ranges. Maximum possible temperature variability within each dinosaur is shown using all isotopic data (black bars), and using the largest difference in the average isotopic values between any two skeletal elements (stippled bars).

have been quite as large as they are today but seasonal climate change was significant. A model of bradymetabolic hadrosaurs weighing between 2 and 5000 kg in such a simulated Cretaceous climate are postulated to have undergone annual variations in body core temperatures of 20-40°C (Dunham et al., 1989). Such temperature fluctuations recorded in the bone phosphate would require intrabone isotopic variability of 4-9‰ and likely 3-5‰ mean interbone variability. This is obviously not the case with any of the Cretaceous dinosaurs. The smaller *Protoceratops* individual and the juvenile hadrosaurs especially are expected to show greater isotopic variability if they had low metabolic rates typical of an ectotherm. It is apparent that the homeothermy seen within the Cretaceous dinosaurs could only have been supported by high metabolic rates. This does not necessarily mean they were the same as modern mammals and birds but they were definitely above those of modern reptiles. The data suggests that body temperature was maintained by a controlled, relatively high metabolic rate.

The Jurassic dinosaurs also appear to be homeotherms. Few bones have intrabone isotopic variability beyond homeothermic limits and the interbone variability indicates homeothermy between body regions. These dinosaurs could also have been endotherms. However, they could also have been mass homeotherms, especially the sauropod, *Camarasaurus*, due to its large size (~15 tons; Gregory Paul, personal

communication, 1993). However, mass homeothermy is only a possibility if the Jurassic paleoclimate of Utah lacked significant seasonality. During the late Jurassic, Utah was located between 15-30°N latitude. Climate during the deposition of the Morrison Formation, from which these specimens came, was semi-arid and seasonal changes were more moisture related rather than temperature related. With the seasonal changes in humidity/aridity, it is likely that much of the isotopic variability in the bones originated from seasonal changes in the isotopic composition of the drinking waters and water ingested in the vegetation (or meat in the cases of *Allosaurus* and *Ceratosaurus*). The similar isotopic variability from the smaller carnivores and the sauropod suggest that this might be the case. Only until a smaller juvenile specimen is analyzed will it be possible to determine if these sauropods grew as endotherms or ectotherms. Similarly, more Jurassic carnosaurs and ceratosaurs need to be analyzed before more conclusive interpretations can be made.

Studies of the isotope compositions of dinosaur bone are just beginning. Already, however, it is becoming apparent that near the end of the dinosaur's reign 65-75 Ma, many dinosaurs were endotherms. They grew rapidly and lived the relatively fast-paced lives of modern mammals and birds. This physiology has implications for their eventual extinction. Could gradual climate change have caused global extinction of such a diverse group of mobile endotherms, or did it take something more drastic such as the hypothesized bolide impact? We still don't know whether or not most dinosaurs were endotherms, nor do we know at what point in time, or how many times it may have evolved in dinosaurs. These and other interesting puzzles pertaining to the life and times of the dinosaurs are waiting to be solved by present and future scientists.

ACKNOWLEDGMENTS

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The Dinosaur Growth Plate:
A Study in Paleohistology

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Paleontologists study past life through analysis of the fossil record. Vertebrate paleontologists are particularly interested in studying those animals with vertebral columns (backbones). The biology of vertebrates is dictated by the millions of cells that make up these complex animals. Histology is the science concerned with the microscopic anatomy of cells, tissues and organs. All life forms are made of cells (membrane-bound bodies within which the chemical reactions necessary to sustain life occur). In complex animals, such as vertebrates, similar cells work together in associations called tissues. Typically, only the harder tissues of the vertebrate body become preserved as fossils. An example of a hard tissue is bone. Our ability to derive information from a fossil is dependent on how well it is preserved and on the techniques we use to study the specimen. Certain fossilization regimes conserve cellular and sub-cellular structure and microscopic examination of appropriately prepared specimens permits detailed study of fossil bone histology (Barreto and Albrecht 1993). The microscopic structure of bone reflects the activity of the cells that produced it. All organisms on earth, and all the cells that compose them are descended from a common ancestral cell; and we have no reason to believe that cells that produced bone millions of years ago were different from bone cells we can study in living animals today. It is possible to compare the cellular structure of well preserved fossil bone to modern bone. Such research, called "paleohistology," allows interpretation of the biology of extinct vertebrates (Reid 1984; Ricqles 1976; Ricqles 1980).

The skeletons of vertebrates are made up of bone and cartilage. Both of these tissues are composed of cells and the substance surrounding the cells (called extracellular matrix) which they produce. It is the extracellular matrix that gives bone and cartilage their familiar attributes. We recognize bone as a strong, rigid material because it is the calcified extracellular matrix of bone cells that we can see grossly. With a microscope, we can see that living bone contains bone cells within this specialized extracellular matrix. Likewise, cartilage is composed of cells encased in their extracellular matrix. The plastic, pearly nature of cartilage is due to the properties of the extracellular matrix. If we look at cartilage under the microscope, we see the cells embedded in the matrix that they synthesize and maintain. It is extracellular matrix that gives bone and cartilage their physical properties including the integrity to withstand the biomechanical forces normally applied to the skeleton as it functions in support of the body and in locomotion.

Bone tissue has diverse biological functions. In addition to the obvious functions of support and locomotion, bone also provides a reservoir for calcium, an element that is critical in many chemical reactions necessary to life. Also, certain blood cells that must be continually resupplied to the body are propagated within bone. All of these functions are studied by bone histologists. We may mistakenly think of bone as a stable tissue, but it is constantly being remodelled by cellular processes which digest old bone and deposit new bone throughout our lives. All cells of the body must work in concert through complex control systems. Histology, therefore, reflects the physiology of an animal. For example, bone histology can be used as an indicator of an animal's metabolism and age. Additionally, abnormal bone histology is diagnostic of certain diseases.

There are various kinds of cartilage in the skeletons of vertebrates. Most contribute to support and locomotion of the body. A special kind of cartilage (growth plate cartilage) is necessary for bones to grow longer (Brighton 1978). Growth plates are discs of cartilage located near the ends of growing long bones. The cells of the growth plate (chondrocytes) have a particular temporal and spatial arrangement and undergo a series of size, shape, and functional changes over their brief life span. Chondrocytes produce, maintain and modify a specialized extracellular matrix vital to the proper function of the growth plate. Each chondrocyte is thus enclosed within a lacuna (cavity) of extracellular matrix. Chondrocytes hypertrophy (enlarge) in the later part of their life and are then called hypertrophic chondrocytes. Hypertrophic chondrocytes eventually calcify their extracellular matrix. Hypertrophic chondrocytes also provide conditions conducive to invasion of the growth plate by blood vessels from the bone shaft. Such vessels contain erosive cells which eat into the calcified growth plate and bone forming cells which produce new bone. The bone forming cells use the calcified cartilage matrix as a scaffold on which to settle and produce new bone. Thus, deposition of new bone on the remnants of the growth plate adds to the length of the bony shaft. The transition point between growth plate and bone is called the chondro-osseous junction. Adjacent to the newly forming bone, the growth plate with the calcified extracellular matrix, would have the greatest potential to be fossilized.

Past phenomena cannot be observed directly and therefore must be interpreted from indirect evidence. Vertebrate paleontologists study fossils to derive information about extinct animals but interpretation of their biology is difficult. Fossilization of vertebrates: is extremely rare and therefore presents a biased sample, is primarily restricted to hard tissues, seldom includes an entire skeleton, and, usually involves postmortem alterations and often mineralization of the original tissue (Behrensmeyer and Hill 1980). Furthermore, the merit of all scientific investigations relies on the establishment of testable hypotheses and this presents a particular obstacle for historical scientists. Obviously, it is not possible to perform experiments to directly measure, for example, physiological attributes of extinct organisms. Therefore, we have to study living animals and compare them to extinct ones. Structures that appear to be identical are said to be homologous when they are present in species that have a common ancestry. Furthermore, it is valid to propose that homologous structures had the same function in extinct and living animals (Rudwick 1985).

Classically, vertebrate paleontologists reconstruct the skeletal anatomy of an extinct animal through study of gross bone morphology and through comparative anatomy with living vertebrates. From skeletal anatomy and biomechanical principals, the musculature, locomotion, strength, mass, and even certain behavioral traits can be inferred. Analysis of the distribution of homologous anatomical characters among taxa leads to the construction of phylogenetic hypotheses, that is, the categorization of organisms based on recency of common ancestry. Phylogenetic systematics is therefore based on acceptance of the concepts of evolution and speciation (Gaffney 1979). Additional information on the biology of extinct vertebrates can be derived from ichnofossils (trace fossils), analysis of fossil site architecture, faunal composition of assemblages, and sedimentology. Upon the discovery of new, more complete, and/or better preserved specimens, the conclusions of paleontological studies can be tested.

Based on gross anatomical evidence, birds can be classified as dinosaurs (Gauthier 1986, Ostrom 1976). The avian skeleton shares a greater number of derived characters with certain theropod dinosaurs than it shares with the skeleton of any other group of animals. The presence of such characters indicates that a common ancestor (in which the traits evolved) gave rise to the group containing both birds and these theropods. One way to test the validity of a phylogenetic hypothesis is to study the distribution of additional

characters. If additional characters are found that are exclusively present in birds and dinosaurs, this would corroborate the hypothesis that birds are indeed members of the dinosaur group. In an effort toward this end, the microscopic morphology of the growth plates of fossil and modern taxa was examined. The dinosaur growth plate was compared, using light and scanning electron microscopy, with those of living taxa with diverse physiological attributes and phylogenetic positions.

Rare and exquisitely preserved vertebrate fossils have been recovered from the Two Medicine Formation of northwestern Montana (Horner 1982; Horner 1988). Included are *in situ* nesting colonies of the duck-billed dinosaur *Maiasaura* (Ornithischia; Hadrosauridae). These sedimentary beds were deposited in the Upper Cretaceous Period, specifically between 84 and 72 million years ago. Light microscopic examination of thin sections of juvenile dinosaur fossils revealed that biological morphology may have been faithfully preserved on a cellular level. In longitudinal section, the architecture of a growth plate interfacing with newly formed bone was evident. Comparison of the microscopic structure of the dinosaur growth plate with the growth plates of a modern mammal, lizard, and bird demonstrated homology of the growth plate in the bird and dinosaur (Barreto et al 1993). The presence of an avian-type growth plate in dinosaurs adds a shared derived anatomical character corroborating inclusion of birds within the Dinosauria.

In general, the morphology of the avian growth plate can be distinguished from that of mammals and lizards when viewed in longitudinal section under the light microscope. The avian chondro-osseous junction describes an undulating line, rather than the straight junction of mammalian and lizard growth plates. In birds, invasion of the growth plate by blood vessels from the bone shaft occurs at spatial intervals so that papillae of hypertrophic chondrocytes become included between the trabeculae (rods) of newly forming bone. In the growth plates of mammals and lizards, the chondro-osseous junction is essentially straight, due to the simultaneous replacement of hypertrophic chondrocytes by bone in a transverse plane (Figure 1).

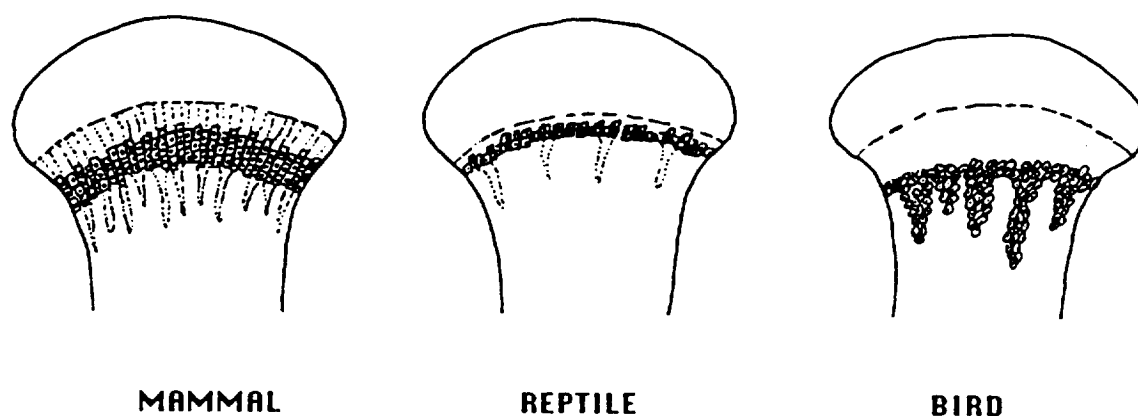MAMMAL   REPTILE   BIRD

Figure 1. Diagram showing some of the basic differences in the morphology of the hypertrophic zone and chondro-osseous junction in the growth plates of a modern mammal, lizard, and bird.

Light microscopic examination of longitudinal sections of the ends of the fossilized juvenile *Maiasaura* long bones reveals the presence of structure we hypothesize to be the hypertrophic zone of the growth plate. The microscopic anatomy looks like a chondro-osseous junction, and our histological interpretation is that the calcified portion of the growth plate has been preserved. In the juvenile *Maiasaura* specimens, the hypothesized zone of calcified cartilage appears as included papillae and islands of clustered hollow, ovoid structures between trabeculae of newly formed bone shaft. The distribution, spatial arrangement, and shape of these lacunae closely resemble the condition observed in birds. Mammalian and lizard hypertrophic chondrocytic lacunae are quadrilateral, and the lacunae in both have a "columnar" organization. In contrast, the hypertrophic chondrocytic lacunae of the dinosaur and bird are oblate spheroids, and a columnar arrangement is not as obvious.

To better see if hypertrophic chondrocytic lacunae were indeed preserved in the dinosaurs, they can be viewed with the greater resolution afforded by scanning electron microscopy. With a scanning electron microscope, we can observe the ultrastructure of the hypertrophic chondrocytic lacunae of modern species. The walls of the hypertrophic chondrocytic lacunae in the calcified part of the growth plate have characteristic bumps called calcospherites. Calcospherites in the mammal and lizard growth plates are present only on the calcified walls of the lacunae. These are the lacunar walls that are parallel to the direction of growth. The walls between lacunae in the same column are thin and uncalcified. However, in the bird, all of the lacunar walls are calcified and have calcospherites. In the dinosaur specimens, the same high degree of structural resolution can be seen as in the modern specimens, and the walls of the lacunae have structures that appear to be identical to calcospherites. These can be seen on all walls, so that the dinosaur and bird lacunae look very similar (Figure 2).

Growth plate morphology varies significantly among species, and morphologic appearance can be translated into differential rates of long bone growth (Hunziker 1988). Growth plate cartilage generates bone elongation in all vertebrates. Lizards grow slowly and retain their growth plates throughout life. The long bones of birds and mammals grow very rapidly in a relatively brief adolescent period. Once adult stature is achieved, the growth plates close. However, it is apparent from their phylogenetic positions, that these two groups of vertebrates have *independently* evolved rapid determinate long bone growth. It is not unreasonable that this coincidental growth pattern is accomplished through different cellular strategies. Recent research has demonstrated some of the differences in growth plate chondrocytic behavior between mammals and birds (Barreto and Wilsman 1994). Such research explains, in part, the distinct histological appearance of mammalian and bird growth plates. Because the growth plates of birds and dinosaurs seem to be homologous, it is possible that their growth plates functioned similarly. Dinosaurs, like birds, may have grown very rapidly over a short developmental period. Once the cellular mechanisms and the controls underlying avian long bone growth are clarified, we can postulate that the same applied in dinosaurs. Paleohistologists apply microscopic techniques that make it possible to add observations on a cellular level to those which can be made grossly on fossil dinosaur bones. With the ability to recognize histological, as opposed to gross morphological structure, new aspects of the biology of extinct animals can be explored.
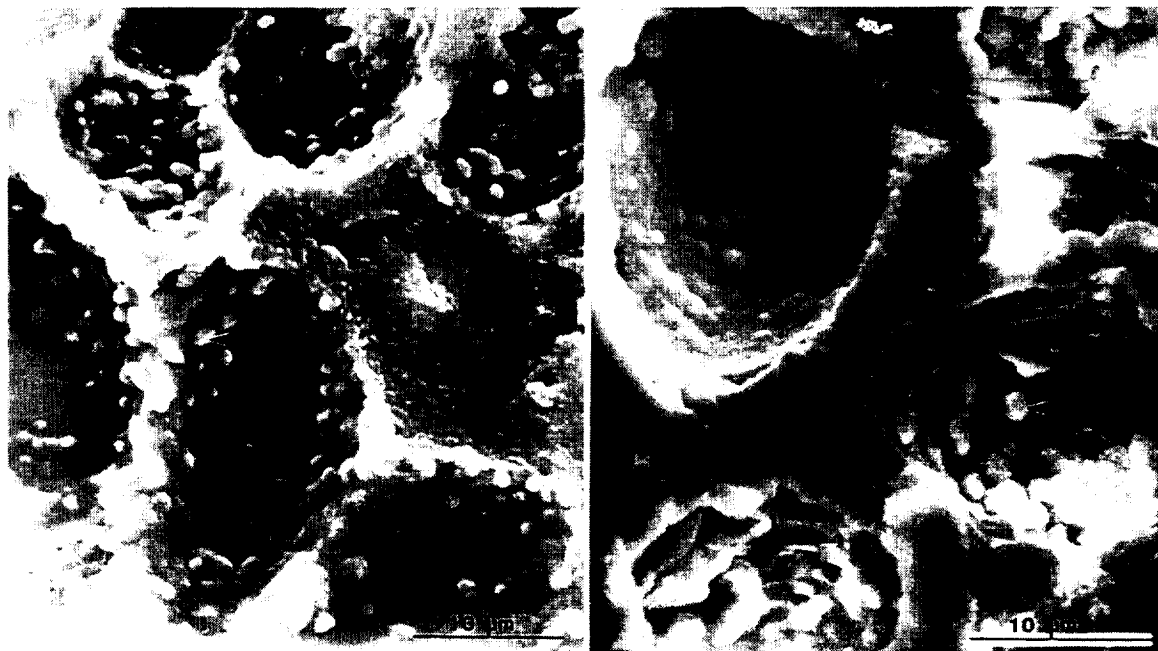
Figure 2. Scanning electron micrographs of the lacunae of hypertrophic chondrocytes from the growth plates of a bird (left) and a dinosaur (right). Calcospherites (arrowheads) are present on all lacunar walls.

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Does the Physiology of Large Living Reptiles Provide Insights into the Evolution of Endothermy and Paleophysiology of Extinct Dinosaurs?

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ABSTRACT

Our studies using American alligators, *Alligator mississippiensis*, green turtles, *Chelonia mydas*, and leatherback turtles, *Dermochelys coriacea*, have provided insights into the physiology of large extant and extinct reptiles. Respiratory and metabolic physiology studies indicate that many living large reptiles exhibit heat conservation adaptations and mechanisms which allow them to maintain constant warm body temperatures in cold environments with low "reptilian" metabolism. For example, leatherback turtles which are found in the oceans as far north as the Arctic Circle can maintain constant body temperatures above 25° C while water temperatures are below 7° C. This dramatic ability to maintain warm temperatures in cold, highly conductive water, that would quickly cause hypothermia and kill most endotherms, is made possible by a mechanism we describe as gigantothermy. Gigantothermy is the ability to maintain constant warm body temperatures with low energy consumption, control of peripheral circulation and extensive insulation due to large body size.

The muscles of leatherbacks show a fiber type unlike the specialized, endothermic heater organs of modern fish Scombroidei (tunas, billfish, bonitos, butterfly mackerel and relatives) that have evolved specialized "endotherm like" red muscle to maintain regional endothermy. The primitive large reptiles like leatherbacks do not show the specialization in muscle fiber type nor do the enzyme activities indicate the emergence or evolution of endothermy or a high rate of energy consumption. Yet leatherbacks can migrate over 70 km per day in the open ocean and dive to depths deeper than 1000 m on a regular basis.

Collectively these physiological studies on large living reptiles support the concept that dinosaurs, especially the larger more spectacular species, were able to maintain high body temperatures, be very active, move great distances quickly, as well as exhibit complex behavior such as communal nesting and nest building

without evolving endothermy or high levels of energy consumption. The physiology of large living reptiles indicates that it is not necessary to attribute heretical ideas to explain the paleophysiology and capabilities of dinosaurs. As reptiles they were fully capable of complex and spectacular behaviors such as long and rapid migrations and surviving the cold. All evolutionary indications suggest that large size would provide a negative selection pressure for the development of endothermy especially in equable and or tropical climates.

INTRODUCTION

The evolution of endothermy has occurred a number of times in vertebrates (Block 1991, Block et al. 1993, Bennett & Ruben 1979). Modern birds, mammals and a few species of fish exhibit true endothermy or "warm bloodedness" the term used by Bakker (1986) and others. Endothermy is defined as the ability of animals to maintain high levels of metabolic activity due to specific elevated enzyme activities, and then to use the heat which is a byproduct of that high biochemical activity to thermoregulate and maintain elevated constant body temperatures independent of the environment. Ectothermy or "cold bloodedness" is the thermoregulatory strategy by which animals utilize external heat and heat conserving mechanisms to maintain body temperatures different than their surroundings. Ectotherms use external heat sources such as solar radiation to elevate body temperatures above ambient or else ectotherms conform body temperatures to that of their surroundings. Ectotherms are incapable of high levels of resting metabolism and must get the heat they use to keep warm from other sources. A third thermoregulatory strategy that is unique to large ectothermic animals is called gigantothermy (Paladino et al.1990) whereby high constant body temperatures are maintained with low, metabolic heat production, the use of large body size to reduce the surface to volume ratio, thick tissue insulation and fine control of peripheral circulation.

Our investigations with turtles, alligators, birds, and elephants have demonstrated that size plays an important role in the thermoregulatory mechanisms employed by terrestrial and aquatic vertebrates (Paladino et al. 1990). Large animals are more isolated from environmental effects on thermoregulation. We have found that large, "cold blooded" ectotherms with a low metabolism, are fully capable of maintaining high constant body temperatures in very cold and highly conductive aquatic mediums and can still reap the benefits of being "constantly warm" without an endothermic, high metabolic physiology (a thermoregulatory strategy called gigantothermy). When compared to small animals with the same general body shape, large animals have less surface area

relative to their increased volume through which they can exchange heat energy. This is the presumed physiological basis for the reduction in the per gram energy consumption as endothermic animals get larger and is referred to as the mouse to elephant curve (Brody 1945, Kleiber 1964) or in the case of reptiles the small lizard to leatherback curve (Figure 1).
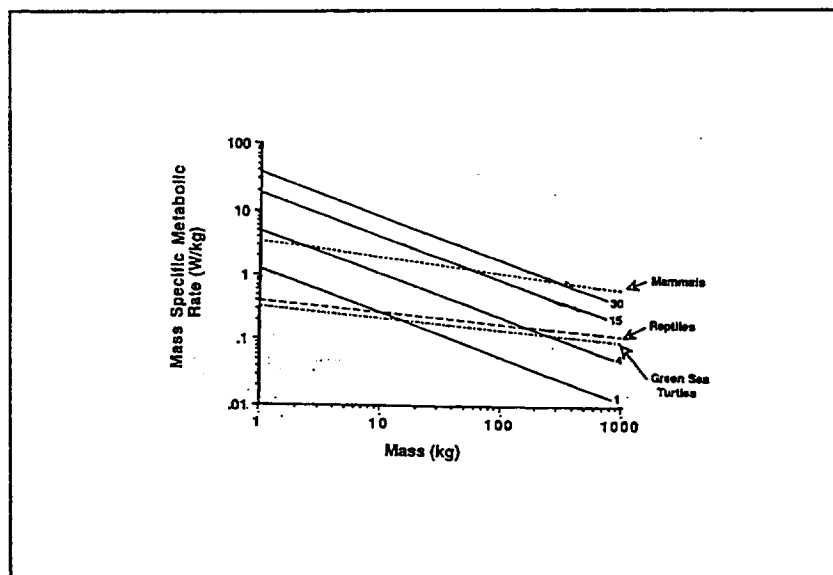
Figure 1   Mass Specific metabolic rates for mammals and reptiles drawn from allometric expressions (adapted from Paladino et al. 1990)

Robert Bakker's (1986) heresies include the statement that large Cretaceous dinosaurs were endotherms. He has based this conclusion on a number of factors which we can investigate using living vertebrates. Some researchers believe dinosaurs were endothermic because of the following assumptions:

1)   Fossil evidence indicates that late Cretaceous dinosaurs lived in the polar more seasonal areas (Rich and Rich 1993, Hammer et al. 1990) where there might have even been snow. Dinosaurs had to be endotherms to accomplish this;

2)   Oxygen 18 isotope analysis for the bones of dinosaurs (Folger 1993, Barrick 1994 this volume) indicates they maintained high constant body temperatures even in their extremities, like modern birds;

3)   Dinosaurs had complex social behaviors such as herding, communal nesting and long distance migrations (Horner 1984) which required them to be endothermic;

4)   Dinosaurs appear to have richly vascularized, dense haversian bone with growth plates similar to those of birds (Barreto et al. 1993);

5)   Birds evolved from small bipedal dinosaurs that diverged from the

dinosaurian lineage more than 90 million years ago; thus all dinosaurs (a monophyletic group) must also have been endotherms since they are the direct precursors of birds;

6) Since dinosaurs were very active, they needed an increased aerobic capacity which necessitated the development of endothermy [the increased aerobic capacity hypothesis for the evolution of endothermy (Bennett and Ruben 1979)].

These are the main arguments that have been used recently in this so called dinosaur endothermy controversy. Other issues crop up as one or more of these arguments become less popular, are discredited, or proven incorrect. We provide data from experiments using large reptiles, fish, and the fossil record demonstrating that all of these arguments do not support the conclusion that dinosaurs had to be endothermic. In fact, all the data, physical principles, theoretical calculations, and physiological evidence to date support the conclusion that large Cretaceous dinosaurs probably were typically reptilian in their physiology. Large dinosaurs were probably gigantotherms with a low metabolism. Most of the data suggest that in the fairly constant tropical to subtropical climates that prevailed during the age of dinosaurs, natural selective forces would have worked against the evolution of endothermy in especially large terrestrial animals. The theoretical and physiological evidence strongly suggests that endothermy would most likely have evolved in dog or turkey sized animals expanding their thermal niches into colder, less constant and more stressful environments.

In our studies we have used leatherback turtles and alligators as models to understand the physiological mechanisms of large extinct reptiles. Leatherbacks can be found in the fossil record in their current form as far back as 20 million years ago (Carr 1952). Despite the fact that turtles split from the stem reptilian line well before the evolution of true dinosaurs (approximately 220 million years BP) their metabolic physiology was probably not significantly different from their dinosaurian contemporaries that were evolving at the same time. Leatherback turtles (Dermochelys coriacea), considered the largest living reptile (Carr 1952), range from the tropics to the Arctic Circle (Willgohs 1957, Bleakney 1965) and are pelagic, eating mostly jellyfish (Duron 1978, Duron & Duron 1980, Mrosovsky and Pritchard 1971). Leatherbacks have been found in cold ocean waters (7.5 ° C) with body temperatures of 25.5 ° C (Friar et al. 1972). These observations, together with data on a leatherback raising its body temperature on land from 29.6° to 30.1 ° C while the ambient temperature dropped from 26.2 to 21.8 ° C (Standora et al. 1984), have resulted in intense interest in their thermoregulatory abilities. We found the resting metabolic rates of these turtles are about one-third the rate of similar-sized mammals (Figure 1). Leatherbacks have vascular countercurrent heat exchangers, an insulating subepidermal fatty layer (Spotila et

al. 1972, 1973), and a large body size, allowing them to maintain body temperatures well above ambient, a thermoregulatory mechanism we call "gigantothermy" (Paladino et al. 1990). Mathematical models (Spotila et al. 1991) indicate that by using large body size, peripheral tissue insulation, and circulatory changes, leatherbacks can maintain warm body temperatures in cold Arctic oceans and not overheat in warm tropical seas (Paladino et al. 1990). On the tropical nesting beaches, leatherback body temperatures are 3 - 10 °C above water temperatures and air temperatures (Paladino et al. 1990) and they thermoregulate by altering circulatory patterns and heat exchange with the environment (Pennick et al. 1994). Other large pelagic aquatic vertebrates such as tunas and other Scombroidei (Carey and Teal 1969,

Figure 2 Comparison of scaled isolated muscle tissue metabolic rates for tuna and turtles (adapted from Pennick et al. 1994)

Carey et al. 1971, Block 1991, Block et al. 1993) are also able to maintain body temperatures well above that of ambient, but they employ true endothermy. Endothermic tunas utilize their centrally placed, highly aerobic red muscle (Figure 2) together with countercurrent heat exchangers to keep warm. Other Scombroidei maintain regional endothermy by utilizing specialized highly aerobic red muscle called heater organs to keep the brain and sensory organs warm. These endothermic thermoregulatory patterns in fish are very different from the mechanism we found in leatherbacks. The fact that an animal maintains a body temperature above ambient does not make it "warm blooded" (Paladino et al. 1990). Warm bloodedness means that an animal is an endothermic homeotherm that has high constant body temperatures, maintained by large amounts of heat derived by internal oxidative metabolism. Large size alone isolates an animal from its environment, allowing internal processes to be relatively independent of fluctuating ambient conditions (Spotila et al. 1972; Spotila et al. 1973; Calder 1984; Spotila et al. 1991). Thus, there should be little difference in the metabolic rates of large mammals and reptiles because gigantism produces similar heat transfer problems, resulting in convergent selection pressures and thermoregulatory strategies that preclude elevated metabolism (Paladino et al. 1990). Metabolic and thermoregulatory mechanisms of leatherbacks have important implications for considerations of size and function of animals
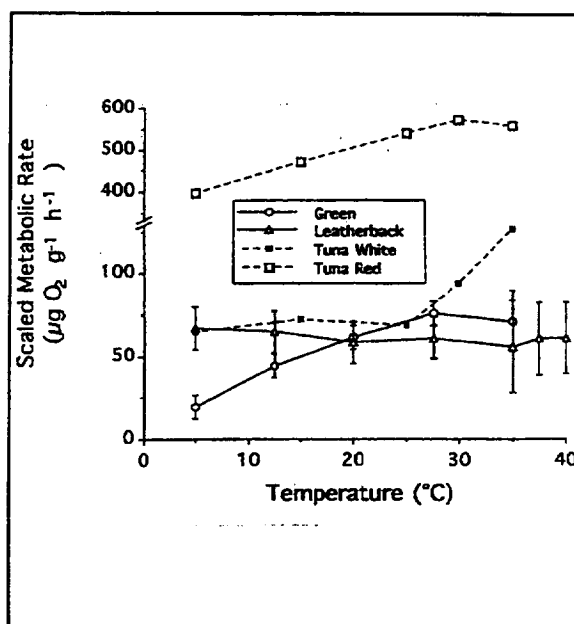
(Paladino et al. 1990), and for speculations on the endothermic capacities of dinosaurs (Spotila et al. 1991, Paladino et al. 1990).

The physiological data and evidence we have gathered from leatherbacks indicate that reptiles with a low rate of metabolism are capable of maintaining high constant body temperatures in the cold aquatic environment of the Arctic Ocean that is even more stressful than the thermoregulatory demands faced by a large terrestrial reptile in the seasonal climates of the Maastrichtian, even in snowy polar regions. These data also provide clear evidence that large dinosaurs found in the more seasonal polar regions did not have to be endothermic to live and thrive, which would rule out argument number 1 as evidence for dinosaur endothermy.

Since gigantothermy would provide a mechanism that would maintain high constant body temperatures, these data further complicate the confusing oxygen 18 isotope argument (Folger 1993; Barrick 1994 this volume). These isotope analyses have been shown in the reviewed literature not to be a good indicator of endothermy. The more consistent oxygen 18 isotope levels in different bones of the same animal at best would be evidence for high constant body temperature and not evidence for how that high body temperature was maintained. Additionally this technique is now very much in doubt because it appears that oxygen 18 isotope varies with latitude and is quite variable in the drinking water at different times. The accuracy of this method for comparing different bones in the same animal has also been questionable at best (Kolodny and Luz 1993). It is quite certain that a large dinosaur even with a low constant metabolism would be capable of maintaining high constant body temperatures with gigantothermy. Therefore these dinosaurs would show high levels of oxygen 18 isotopes throughout their bones because they were constantly warm, not "warm blooded". Thus argument number two also bites the dust.

We have data that show leatherbacks have very specific migratory routes that cover thousands of kilometers (Figure 3). These complex, long distance migrations include turtles traveling, on the average, 70 km per day, not including the up and down movements during that period. The complex migrations of sea turtles include massive social nesting behaviors called "arribadas" whereby tens of thousands of sea turtles emerge together on the same night to lay their eggs in nests concentrated in a small area of beach. When these coordinated migratory behaviors are coupled with the nestbuilding and nest protection behavior of alligators, a repertoire of complex behaviors emerges, not unlike the migration, communal nesting and nestbuilding of *Maiasaura* described by Horner (1984). Alligators have complex behavioral, energetic and physiological thermoregulatory mechanisms (Terpin et al. 1979), and also respond to auditory cues from their eggs and hatchlings, and defend their vegetative mounds in a manner similar to

what may have occurred with these dinosaurs. It has also been suggested that these vegetative nest mounds serve to maintain egg temperatures critical for proper and more rapid incubation. These complex nests may be necessary to regulate incubation temperatures in order to provide correct developmental temperatures for production of both males and females in an organism with Temperature - Dependent Sex Determination (TSD). We postulated that dinosaurs may have also had TSD, as in crocodiles, alligators, and sea turtles (Paladino et al. 1991). These complex behaviors such as herding (arribadas in sea turtles), communal nesting, and complex nest building and hatchling care (nesting beaches for turtles and vegetative nest building and nest and hatchling defense in alligators), as well as long distance, very specific migration routes can all be found in current day reptiles.

Figure 3   Satellite movements of two post nesting female leatherback turtles (dashed line = transmitter # 2105, solid line = transmitter # 2106) in the Pacific Ocean. Satellite track lasted for longer than 2000 km and 60 days.

There is no need to be "warm blooded" or endothermic to exhibit these complex behaviors. These data provide an abundance of evidence to counter argument number 3 above.

Recent discoveries in the field of bone histology by Chinsamy et al. (1994) indicate that ancestors of current endothermic birds, a hen sized Cretaceous bird called *Patagopteryx deferrariisi*, plus two species of Enantiornithene birds had growth rings or lines of arrested growth (LAGs) characteristic of ectothermy and/or seasonal growth. LAGs have also been found in zonal bone of non - avian dinosaurs (Reid 1990, Chinsamy 1990), indicating that this line of evidence for endothermy in birds is marginal at best. Chinsamy et al. (1994) concluded that the bone histology of Mesozoic birds indicates that endothermy and the azonal growth pattern typical of modern birds probably evolved well after birds split from the dinosaur lineage, and well after they had evolved feathers and the capacity to fly. Additional arguments using bone histology as evidence for

endothermy in dinosaurs was recently presented by Barreto et al. (1993). This study compared the cartilaginous growth plates of an adult monitor lizard, a 8-10 month old dog, a two week old chick and a hatchling dinosaur. They concluded that since the growth plates of two week old bird and hatchling *Maiasaura* (Ornithischia: Hadrosauridae) were most similar, and that the adult modern lizard and juvenile dog had a more linear growth plate, that this was evidence for very rapid growth in hatchling dinosaurs similar to the pattern in modern birds. It then followed that dinosaurs, must have also been endothermic. The experimental design did not include a disciplined comparison of the growth plates of juvenile lizards like *Varanus, Agama* and *Chamaeleo* in which young individuals have well developed cartilaginous canals and irregular growth plates similar to those seen in newborn mammals as well (Haines 1941, 1942, 1969). Thus the reported similarities may result from inappropriate comparisons of ontogeny rather than indicating phylogenetic or physiological similarity. When incomplete histological comparisons like those made by Barreto et al. (1993) are made across phylogenetic lines, care should be taken to ensure that similar aged individuals at similar stages of development are made. After careful examination of the fossil and present day bone histology of dinosaurs, fossil birds, living birds and living reptiles, it appears that this line of so called endothermy evidence (argument #3) from above also has mixed results at best, and most likely points to the evolution of endothermy in birds well after they split from the dinosaur lineage.

Both the bone histology (Chinsamy et al. 1994) and the reptilian muscle power physiology (Ruben 1991) indicate that flapping flight probably evolved in primitive birds before endothermy. It appears that endothermy probably evolved well after birds split from the dinosaur lineage and well after the evolution of flight. Endothermy was not a necessity for the evolution of flight (increased aerobic capacity argument), and the muscle physiology of a reptile is fully capable of launching a primitive chicken - to turkey - sized bird into the air from the ground (Ruben 1991). A chicken - to turkey - sized bird does not use the constant highly aerobic flapping flight we see in the small migratory birds of northern temperate climates. Larger birds use short bursts of their wings to propel them up where they can then glide, and also use intermittent bursts, or thermals to fly long distances. Vultures, eagles, and hawks can migrate great distances without the need for continuous flapping flight. We suspect that the primitive birds of the same size that evolved from a chicken - to turkey - sized bipedal dinosaur probably could do the same thing. Birds may have evolved endothermy to expand their niches into the more seasonal northern and southern latitudes that became much colder as cooler climates changed in the Maastrichtian. These primitive birds would have then needed to maintain constant high body temperatures to ensure that their high power, reptilian muscles were kept warm in the cold. Keeping these reptilian muscles warm was necessary to generate the thrust to get airborne. A chicken - to turkey - sized bird would

have required endothermy to keep their muscles warm in colder climates. Once endothermy evolved in these medium to large primitive birds, smaller birds with an even greater endothermic capacity could then also expand their aerobic scope to support the typical high energy flapping flight that we see in the small northern temperate species of today.

This scenario of thermoregulatory selection pressures and thermal niche expansion may have been the driving force in the evolution of endothermy in birds. These arguments would provide additional support for the hypothesis of Block et al. (1993) that endothermy in fish evolved as a result of niche expansion, and not the need to support higher aerobic capacities. In the monophyletic Scombroidei, endothermy has evolved at least three separate times (Figure 4 drawn from Block 1991, Block et al. 1993). This phylogeny was generated by genetic comparison of the cytochrome b gene using PAUP computer program. Identified at points A, B, C, and D are inferred evolutionary developments of endothermic red muscle. In each case the modification involved a different mechanism: A = modification of the superior rectus muscle into a thermogenic organ (countercurrent heat exchanger formed from the carotid artery); B = modification of the lateral rectus muscle into a thermogenic organ (heat exchanger derived from the lateral dorsal aorta); C = systemic endothermy using vascular counter current heat exchangers in the muscle, viscera, and brain (heat exchanger in the brain is formed from the carotid artery); D = some internalization of red muscle along the horizontal septum. The genetic outgroups used for comparison are all fish ectotherms with laterally placed red muscle (Sphyraena, Serranidae, and Coryphaena). Close relatives of the tuna, such as bonitos also swim very rapidly but are ectothermic (Figure 4). Tunas
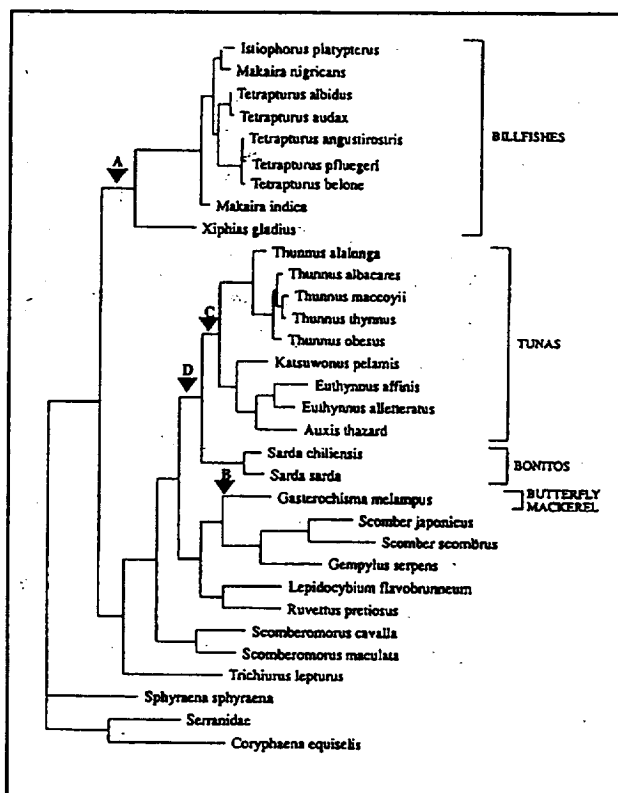

Figure 4 Phylogeny of the Scombroidei from Block et al. 1993. Genetic comparison of cytochrome b using PAUP. A, B, C, and D = inferred evolutionary developments of endothermic red muscle.

on the other hand are true endotherms, with thermally isolated and specialized red muscle that has exceptional aerobic capacities. These changes allowed tunas to expand their thermal niches into the colder northern and southern oceans as well as much deeper than their ectothermic relatives, the bonitos. Leatherbacks, on the other hand, use a constant low wattage power supply to fuel their very active long distance migrations, and to dive to depths greater than 1000 meters in the cold ocean (Figure 2). The Scombroidei fish data, data from a gigantothermic turtle, reptilian muscle power calculations, and the fossil bone histology of dinosaurs and primitive birds all suggest that arguments # 4, 5, and 6 are not supported by the data from living and extinct reptiles, birds, dinosaurs and mammals.

In conclusion the preponderance of the data and evidence indicate that large Cretaceous dinosaurs probably were not endothermic. With a reptilian physiology, large dinosaurs were fully capable of complex behaviors, thermoregulation in colder, more seasonal environments, high levels of activity and even flight. The evidence also indicates that there would have been strong selection pressure against endothermy in large Cretaceous terrestrial animals. In the fairly constant tropical and subtropical climates of the Cretaceous, it would have been difficult for a large endotherm to survive due to overheating (Spotila et al. 1991). The average large terrestrial birds and mammals that have evolved are typically half the size of Cretaceous dinosaurs (Dodson et al.1990, Farlow 1993). Extinct giant birds and mammals also evolved in more seasonal and much colder climates than the dinosaurs experienced and yet endothermy probably prevented them from getting much larger than what is possible today in elephants. It is only when an endotherm has a large heat sink such as in cold water that they can achieve the mammoth proportions as we see in cetaceans, seals, and walruses. These marine mammals can take advantage of the great primary productivity in the cold oceans and also dissipate the great heat loads that their huge endothermic mass produces. Today large marine mammals are not typically found in tropical oceans except to calf. Thus we conclude that dinosaur endothermy is in no way supported by sound scientific data or on a theoretical basis.

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Paleopathology and the Sexual Habits of Dinosaurs, as Derived from Study of Their Fossil Remains

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INTRODUCTION

Dinosaurs, medicine, and pathology and have long been intertwined. A family physician, Gideon Algernon Mantell, found the first English dinosaur, while making house calls (Rothschild and Martin, 1993). This was 19 years prior to Sir Richard Owen's first use of the name, dinosaur in 1841. The Carnegie Museum's acquisition of its superb *Tyrannosaurus rex* skeleton was the result of another form of pathology. Fear that Hitler would bomb New York City led The American Museum of Natural History to transfer one of its two tyrannosaurs (to safeguard the genus).

If you don't know history, you are condemned to repeat it. Such is one of the premises for study of ancient disease, the science of paleopathology. Isolated reports of injuries and bone fusions (Moodie, 1923) in dinosaurs were initially treated as curiosities. The current approach is to examine pathology as a population phenomenon. This has proven as insightful to dinosaur lifestyle and behavior (Rothschild and Martin, 1993), as has the trackway analyses reported by Lockley (1986). While it is intriguing to better understand ancient organisms and their life stresses, so much more important is it to learn from their "successes and mistakes." While paleopathology can be explored from a number of perspectives, "defleshed" bones are frequently all that is available to the paleontologist. In spite of this limitation, microstructure and even antigenicity are often well preserved (Rothschild and Martin, 1993). Immunologically identifiable collagen has even been extracted from 100 million year old bone. Although dinosaur DNA has yet to be identified, let alone analyzed (Jurassic Park, aside), 25 million year old insect DNA has been extracted, cloned, and compared to that from contemporary insects (Poinar and Hess, 1982). It is the lifestyle insights that are now explored.

AVASCULAR NECROSIS

Bone pathology often reveals a great deal about the life style of the affected group. Avascular necrosis produces bone death and loss of bony matrix in a linear pattern at the periphery of the original blood supply (Rothschild and Martin, 1993). This is recognized on x-ray as a radiolucent (clear) zone and on gross exam as collapse of subchondral (the bone just under the cartilage of a joint) bone (Figure 1). First noted in free-diving humans (Pauley, 1965; Strauss, 1970), it has also been clearly documented in Cretaceous (65 million years before present) mosasaurs and marine turtles from the Cretaceous through Holocene (contemporary) (Rothschild and Martin, 1993). Universally present in *Platecarpus* and *Tylosaur*, it was absent in *Clidastes*. It was present in *Platecarpus*, *Tylosaur*, *Mosasaurus*, *Plioplatecarpus*, *Prognathodon*, and *Hainosaurus*, but not in *Clidastes*, Ectenosaurus, or *Halisaurus*. Occurrence in a genus was independent of locale. European and North American representatives were equally affected. The only viable explanation is decompression syndrome (Rothschild and Martin, 1993). Repetitive diving, with only short surface intervals is suggested as the cause. The food chain is probably the proximal cause. If individuals were being chased by the Cretaceous analog of the great white shark, they may not have listed adherence to diving tables as their top priority. If an individual were following a meal, they may also not have been attentive to such details.
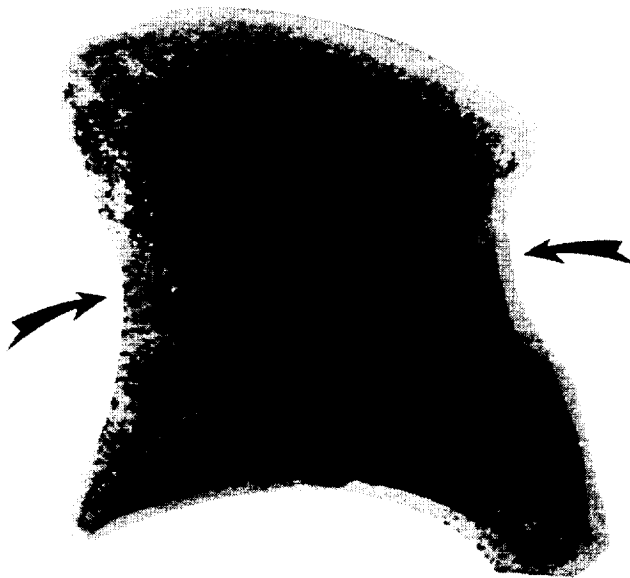

Figure 1. X-ray of *Platecarpus* vertebrae seen in lateral projection (University of Kansas Museum of Natural History). Band of reduced density (arrow) and lost definition of bony structure transects the vertebra.

Avascular necrosis was notably lacking in plesiosaurs, early ichthyosaurs, champosaurs, and claudiosaurs. It is unclear whether these were not repetitive divers (as were many genera of mosasaurs), or if they had derived an effective protective/defense mechanism [which prevented the development of avascular necrosis (and by presumption, bends)]. As it has been hypothesized that morphologic and functional adaptations prevent most diving vertebrates from routinely succumbing to decompression syndrome (Kooyman and Sinnett, 1982), study of the prehistoric distribution of avascular necrosis may allow evolution of those defense mechanisms to be recognized.

ARTHRITIS

The spectrum of arthritis amenable to assessment in ancient individuals is actually limited, as most of the 100 plus varieties of arthritis are not known to produce any bony alterations (Rothschild and Martin, 1993). Osteoarthritis, the most common form of arthritis in humans, was actually quite rare in dinosaurs (Rothschild, 1990; Rothschild and Martin, 1993). The previous misconception, that osteoarthritis was common in prehistoric animals (Abrams, 1953) was related to a semantic error. Although the term osteoarthritis has been applied to describe osteophytes (spurs) affecting vertebral centra, the more correct term for that phenomenon is probably spondylosis deformans. Osteophytes on movable cartilage-lined joints are more properly considered evidence of osteoarthritis. As spinal osteophytes are asymptomatic, except when they impinge on spinal nerve roots, they further differ from osteoarthritis by lack of clinical significance. There are only two known examples of osteoarthritis that have been found in the remains of over 10,000 dinosaurs (Rothschild, 1990). Osteoarthritis in the ankles of two *Iguanodon bernissartensis* (in a herd numbering 39 individuals) are the only known occurrences (Rothschild and Martin, 1993). The sauropods were specifically spared (Rothschild, 1990). Limited occurrence of osteoarthritis in massive dinosaurs suggests that a protective mechanism was operative. As osteoarthritis commonly complicates joint laxity in human and animal models, perhaps the range of motion of weight-bearing dinosaur limbs was constrained to a hinge function (precluding laxity). Osteoarthritis has been observed in pterosaurs (Bennett, 1994). However, pterosaurs are not actually dinosaurs but flying lizards. The osteoarthritis was present in one genus, *Ornithocherius*, localized to the carpal-metacarpal joint. It was recognized by the grooves formed by loss of cartilage with bone rubbing on bone. One interpretation relates to the importance of this joint in pterosaur flight. This was an evolutionary, but biomechanically inferior attempt to develop a functional flight-permitting wrist. Absence of evidence of osteoarthritis in another genera of pterosaur, *Pteranodon*, may reflect less flight activity in that group.

FRACTURES

Fractures of forelimb and feet are common among carnivorous dinosaurs (Molnar and Farlow, 1990). While considered by many simply a hazard of food acquisition, Vance (1989) suggested that fractures might be related to mating activities. Tanke (1994) performed the only systematic studies of fractures in herbivores, studying ceratopsians and hadrosaurs from Alberta. He found fractures in 0.025-1% of ceratopsians (*Centrosaurus* and *Pachyrhinosaurus*), predominantly localized to mid and posterior dorsal ribs. This pattern was quite similar to that noted in male American Buffalos, which McHugh (1958) attributed to the flank butting (involved in establishing "sexual priorities"). The distribution of fractures in hadrosaurs was predominantly to proximal caudal neural spines (Rothschild and Tanke, 1992). These injuries appear related to mating activities (impact of the male on the female's tail and neural spines. Such lesions in *Camptosaurus browni* and *Iguanodon* have been similarly attributed (Blows, 1989; Gilmore, 1909).

DIFFUSE IDIOPATHIC SKELETAL HYPEROSTOSIS

Diffuse idiopathic skeletal hyperostosis or DISH is a phenomenon wherein ligaments and tendons calcify at their points of attachment to bone (Rothschild and Martin, 1993). Actually they do not just calcify, but take on the form of normal bone, with all the appropriate microstructure. While such ossification may be distributed to various areas of the skeleton, involvement of spinal longitudinal ligaments is especially pertinent to study of dinosaurs. The longitudinal ligaments are positioned parallel to the long axis of the vertebral column. Their function appears to be maintenance of normal vertebral column alignment. The ligamentous ossification that characterizes DISH appears as a tortuous paravertebral calcification. It is localized predominantly anterior and lateral to the vertebral centra (affecting the anterior longitudinal ligament and lateral longitudinal ligaments, respectively), but can occasionally affect the posterior longitudinal ligament. This ossification often appears as if candle wax has dripped down the vertebrae (Rothschild and Berman, 1991). The joints of the axial skeleton are spared. There is no zygapophyseal (facet) or sacroiliac joint damage.

DISH is a purely ligamentous phenomenon. While the earliest sign of DISH appears to be formation of new bone next to the mid-section of a vertebral body, the ossification is essentially separate from the actual vertebral centra. DISH is recognized on x-rays as a dense, occasionally thick line (up to a centimeter thick) which parallels the vertebral column. Its separation from the vertebral bodies themselves is recognized by a lucent area between the ossification band and the vertebrae (Rothschild and Martin, 1993).

DISH is not a disease in humans. While diabetes, or at least elevated blood sugars, may be associated with DISH in humans, there is no evidence that DISH is harmful (Rothschild, 1985; Schlapbach et al., 1989). Actually, DISH appears to prevent problems. People with DISH have less back and neck problems than individuals without DISH. Thus, it appears appropriate to consider DISH a phenomenon rather than a disease (Rothschild and Martin, 1993).

While DISH is not a disease, several diseases can be confused with DISH. Infection of vertebrae may cause a "congealing" or coalescence with a spongy bone reaction (Rothschild and Martin, 1993). This is not a ligamentous problem and thus can readily be distinguished from DISH. One family of arthritis, however, may have changes which can be confused with DISH. Spondyloarthropathy includes such diseases as ankylosing spondylitis, psoriatic arthritis, inflammatory bowel disease, and reactive arthritis. While the specific characteristics that distinguish one from another in this group are not important, all can cause ligamentous fusion. However, that ligamentous fusion is associated with other vertebral changes. Erosion and fusion of zygapophyseal joints and direct bony bridging between the anterior or lateral borders of adjacent vertebrae are characteristic of spondyloarthropathy (Rothschild and Martin, 1993). Absence of the latter facilitates identification of DISH.

Purely ligamentous ossification identifies DISH and perhaps two other phenomenon: Fluorosis and hypervitaminosis A. Fluoride produces dense, but quite brittle bone. The brittleness relates to the disturbance of normal bony architecture. DISH-affected ligaments consist of normal Haversian bone. The component structures of normal Haversian bone have an onion-skin or lamellar appearance, especially recognizable on polarizing microscopy (Rothschild and Martin, 1993). This architecture is lost, such that the bone appears quite "chaotic." Excess ingestion of fluoride also increases the density of bone, so they become heavier and are less penetrated by x-rays. Excess vitamin A ingestion does not produce dense bone, but it does produce the same chaotic, non-lamellar architecture in the ossified ligaments (Rothschild and Martin, 1993). Hypervitaminosis A would be important to hypothesizing paleontologic behavior (should it be observed), as such intoxication has been noted when carnivore liver is ingested (e.g., Arctic explorers who ate polar bear liver).

What does all this have to do with dinosaurs? Actually, ossified spinal ligaments with normal lamellar Haversian systems were present in most dinosaurs (Rothschild and Martin, 1993). This phenomenon occurs early in ontogeny, recognized even in juveniles. Recognition of ossified longitudinal ligaments (DISH) in ceratopsians (horned dinosaurs), hadrosaurs (duck billed dinosaurs), iguanodonts (the only dinosaurs known to develop osteoarthritis), and pachycephalosaurs (head butters) (Figure 2) perhaps explains trackway observations. Although dinosaurs were once thought to be "tail draggers," it has been very difficult to identify any evidence of "tail drag" marks on known trackways. Thus it was speculated that the dinosaurs kept their tails in the air. Anterior longitudinal
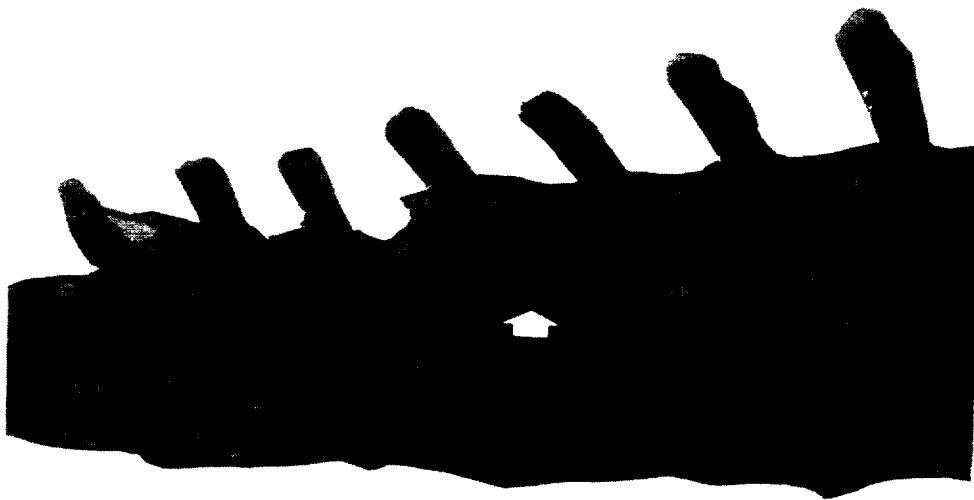
Figure 2.   Lateral view of *Camptosaurus* caudal vertebra.   (American Museum of Natural History).   Ossified ligaments (arrow) are noted anterior and lateral to the vertebrae.
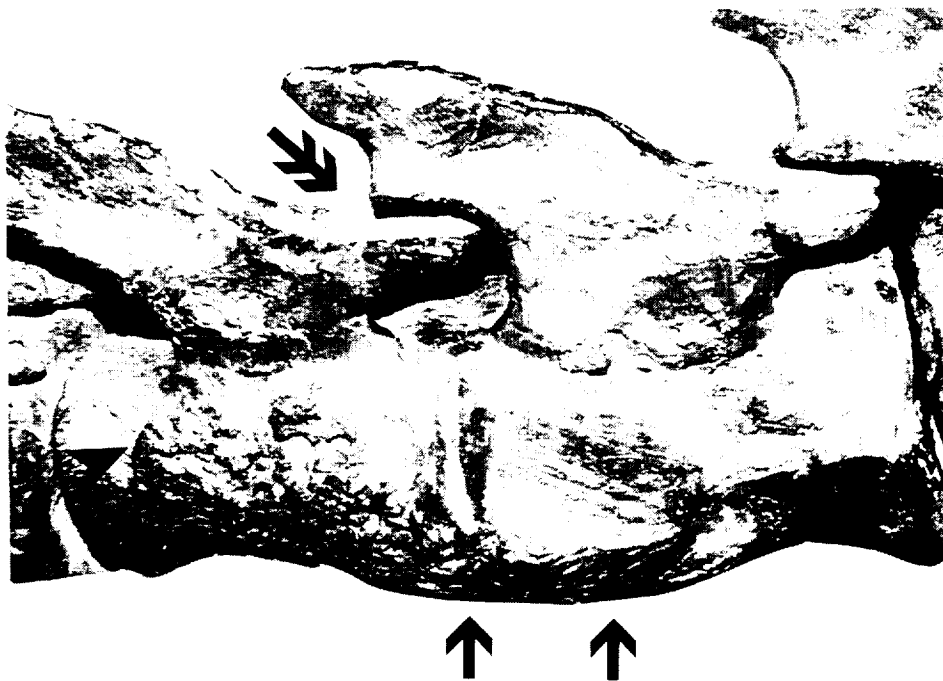

Figure 3.   Lateral view of *Apatosaurus* vertebrae.   (Carnegie Museum of Natural History).   Two vertebrae are bridged inferiorly by a band of bone (arrow).   Slight adherent ossified ligament (arrowhead) is also noted on the vertebra on the left. The posterior, zygapophyseal, joints (double arrow head, uppermost in photograph) are normal.

ligament ossification certainly facilitated that position, preventing "droop." However, ossification of lateral longitudinal ligaments has another effect. It stabilizes lateral movement. Not surprisingly, stegosaurs (which swung their tail as a weapon) did not have ligamentous ossification. Ankylosaurs utilized ligamentous ossification for a special protective function. Fusion of the distal caudal vertebrae occurred in select ankylosaurs, those with "clubs."

Sauropods perhaps had the most specialized version of ligamentous ossification or DISH. Fusion of two to four caudal vertebrae was present in 50% of *Diplodocus* and *Apatosaurus* and 25% of *Camarasaurus* (Figure 3) (Rothschild and Berman, 1991). As its frequency distribution had interesting implications, certainty of diagnosis was critical. The possibility was suggested that this "damage" had occurred when sauropod dinosaurs reared up on their hind legs (ala Barosaurus at the American Museum of Natural History). Had this been a response to trauma or injury, other areas would certainly have been affected. The zygapophyseal or facet (posterior joints of the vertebrae) are quite gracile and would have been injured, before the main body of the vertebra was affected. Preservation of uninjured zygapophyseal (facet) joints in sauropods with vertebral fusion, even at the sites of fusion, eliminates that possibility (Rothschild and Martin, 1993). Further proof was desired. The question was raised as to where the fusion took place. Was it through the center or edges of the vertebrae or was it actually a ligamentous phenomenon? The specimens were actually quite heavy and routine x-rays did not provide sufficient detail. As we did not wish to routinely perform destructive analysis on a non-renewable resource (the fossil), the next approach was computerized tomography or CAT scan. The scans revealed separation between the ossified ligaments and the vertebral centra. Sectioning one specimen confirmed the ligamentous nature of the calcification and histologic examination confirmed normal bony structure. The diagnosis of DISH was established.

This ligamentous ossification, however, was very focal in its distribution. It occurred only in caudal vertebrae and only in those positioned 17-23 segments caudad to the sacrum. This location, approximately two-fifths of the way down the tail is the site where buttressing is placed in building cantilever bridges. It provides major structural support, reducing the tendency towards sagging of more distal structures. The fusion facilitated a tail elevated position, as also suggested by the trackway record (Bakker, 1968; Thulborn, 1984). While a defensive use of the tail (e.g., to whip carnivorous dinosaurs) had been hypothesized (Hatcher, 1901), the population frequencies suggest a sexual dimorphism. Sexual dimorphism implies that it was either a male or female trait. Such has been found for DISH in humans. While DISH in sauropods could be related to intra-species territorial or courting competition, the suspicion is that it was integral to the mating act (Rothschild, 1987; Rothschild and Berman, 1991). Any condition which produced greater stiffening of the tail in the female would maintain the cloaca in a position more accessible for mating. We therefore suggest that the ligamentous ossification (present in

50% of *Diplodoccus* and *Apatosaurus* and 25% of *Camarasaurus*) identifies the females of the species.

SUMMARY

Collaborative investigations by paleontologists with students of medicine permit speculation on diagnosis, its verification and assessment of its significance for prehistory and for contemporary practice. While diagnoses may appear obvious, verification is an essential step. Let us reflect together on the implications of the past.

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On the Elusive Trail of Fossil Dung

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INTRODUCTION

Every once in a while, prospecting paleontologists happen upon distinctive fossil blobs with vaguely familiar shapes. They are usually sausage-shaped or roundish, and are made of material that is clearly not just bone or parent sediment. These unusual formations are fossil feces—also known as coprolites. They were produced by fish, crocodiles, and mammals, and some were produced by dinosaurs.

All animals regularly rid themselves of the unusable byproducts of digestion and metabolism. In other words: if one eats, one excretes. We know that all extant and extinct vertebrates have produced metabolic wastes, often in solid form. In most situations we regard fresh fecal calling cards as amusing or annoying, yet they have the potential of providing valuable biological information about extant animals. This unlikely source of data may also prove to be effective in studying extinct animals. The problem is that fossil droppings may be even more elusive and difficult to understand than the fossil skeletons of the animals that produced them. In the first place, they have usually been altered in appearance and composition through time. Furthermore, as trace fossils (fossils recording biological activity), they are not actual body parts, but instead provide evidence indicating the activity of prehistoric animals. These traces can provide paleobiological information that is unavailable from body fossils, but the study of such fossils is different than the study of skeletal fossils, and care must be taken so that their paleoecological implications are not overinterpreted. So what can we deduce from these mementos that were long ago discarded by ancient animals?

WHY STUDY THE STUFF THAT'S LEFT BEHIND?

In order to learn what coprolites can tell us, we must first understand what recent animal droppings consist of, and what we can learn from them. Feces are the discarded end products of the digestive process. Fecal composition is highly variable (depending on diet, type of organism, and the efficiency of digestion)

but generally includes sloughed cells, mucus, digestive secretions, microorganisms, and undigested food items. Although most nutritive components of ingested food have already been extracted during passage through the gut, valuable clues to feeding habits are often found in the waste. These residues frequently include structural components of organisms that are not easily broken down. For example, while the proteinaceous meat fraction of a carnivore's diet is easily digested, skeletal elements are highly resistant. As a result, many carnivore scats contain fragments of bone and teeth.

Durable components of a herbivorous diet are also found in fecal material. Structural compounds of plants include cellulose, hemicellulose, and lignin—complex polysaccharides that are responsible for the rigidity of plant organs like leaves and stems. Although cellulose and hemicellulose can be digested with the aid of fermentative gut microorganisms, these substances are difficult to break down, and the extent of degradation depends on the architecture of the digestive system, the percent of fiber in the food, and the residence time in the gut. Herbivores that eat highly fibrous plant materials must consume large quantities in order to meet their energy needs. This means that they also excrete significant amounts of fecal material that may appear little altered from its original state (facts easily verified by anyone who has spent time around horses!).

Because undigestible structural residues can be found in fecal material, the examination of recent droppings can provide valuable information on animal diets. Wildlife biologists frequently use this technique to help determine the eating habits of free-ranging animals from tortoises to gorillas. Extended studies of this type can also detect whether there is seasonal variation in the diet. An eleven-year scat survey, for example, indicated that Yellowstone grizzly bears tend to feed on ungulates in early spring, grasses in late spring, and pine seeds in the fall (Mattson et al., 1991). Such long-term observations clarify trophic (feeding) relationships in the ecosystem. In addition to dietary components, the study of droppings contributes other types of information, including population estimates, parasite identification, and medical data. Of course, such information is most useful if the scat producer is known. If the actual deed was not observed, researchers can often pinpoint the responsible animal by using biochemical analyses (e.g. Major et al., 1980).

Thus, under the best (freshest) of circumstances, scat in the field may provide important information on the biology of extant animals. Unfortunately, the same quality of information is not available from droppings that have been reposing for tens of millions of years. Because fecal material is primarily composed of unmineralized tissues, it is not often preserved, and the specimens that survive intact may look significantly different than when they were first deposited.

Nevertheless, ancient feces have been discovered. Even two week-old animals scats may be difficult to identify, so one can appreciate the early scientists who were able to recognize feces originally deposited many millions of years ago.

THE EARLIEST RECOGNITION OF FOSSIL FECES

The first scientist to recognize fossil feces was the Reverend William Buckland, a competent though quirky scientist who enjoyed offbeat geological problems (Pemberton and Frey, 1991). Buckland is often remembered as one of the first paleontologists to describe dinosaur fossils--even before the term "dinosaur" had been invented (Buckland, 1824). One of his research projects was the study of a cave at Yorkshire, England containing fragmented fossil bones and teeth from a broad assortment of animals including hyenas, elephants, hippopotami, tigers, deer, rabbits, mice and birds (Buckland, 1823). Buckland deduced that the cave had functioned as a hyena den where many carcasses had been consumed. It was here that Buckland found some small white balls which he interpreted as hyena feces. He reasoned that the balls had the same mineral composition as bone because the hyenas ingested quantities of bone while feeding. Buckland called these fossils 'album graecum', and tested his hypothesis by comparing the cave balls with fresh hyena scat. The similarity was evident, and his 1823 report on the hyena den represents the first recorded identification of fossil feces.

Although Buckland recognized the ancient 'album graecum' at Yorkshire, he did not introduce the term 'coprolite' until 1929 when he encountered much older feces in the Jurassic sediments of Lyme Regis (Buckland, 1835). This area was well-known for its ichthyosaur fossils and people had already noticed that peculiar rounded bodies were often found in association with fossil bones. Buckland noted that these objects resembled "oblong pebbles or kidney-potatoes" (Figure 1) and initially thought they were clay concretions. He must have recalled the contents of the hyena den, however, because he eventually deduced that these mysterious blobs were also fossil feces. These new samples were more elongated than the hyena droppings and had a distinctive spiral configuration evident in cross-section. Because they were often found in the abdominal region of ichthyosaurs, Buckland proclaimed these newly named 'coprolites' had been produced by those marine reptiles. Now we know that such spiral coprolites were deposited by primitive fish (Woodward, 1917). Yet, despite his error in attributing the Lyme Regis coprolites to ichthyosaurs, Buckland's recognition of fossilized feces was no small feat. Others had observed coprolites without realizing what they were. Famed fossil hunter, Gideon Mantell (1822), had speculated that the spiral formations he examined were fruits or cones, although he acknowledged that their composition was the same as that of bone. The discovery of coprolites added a new dimension to
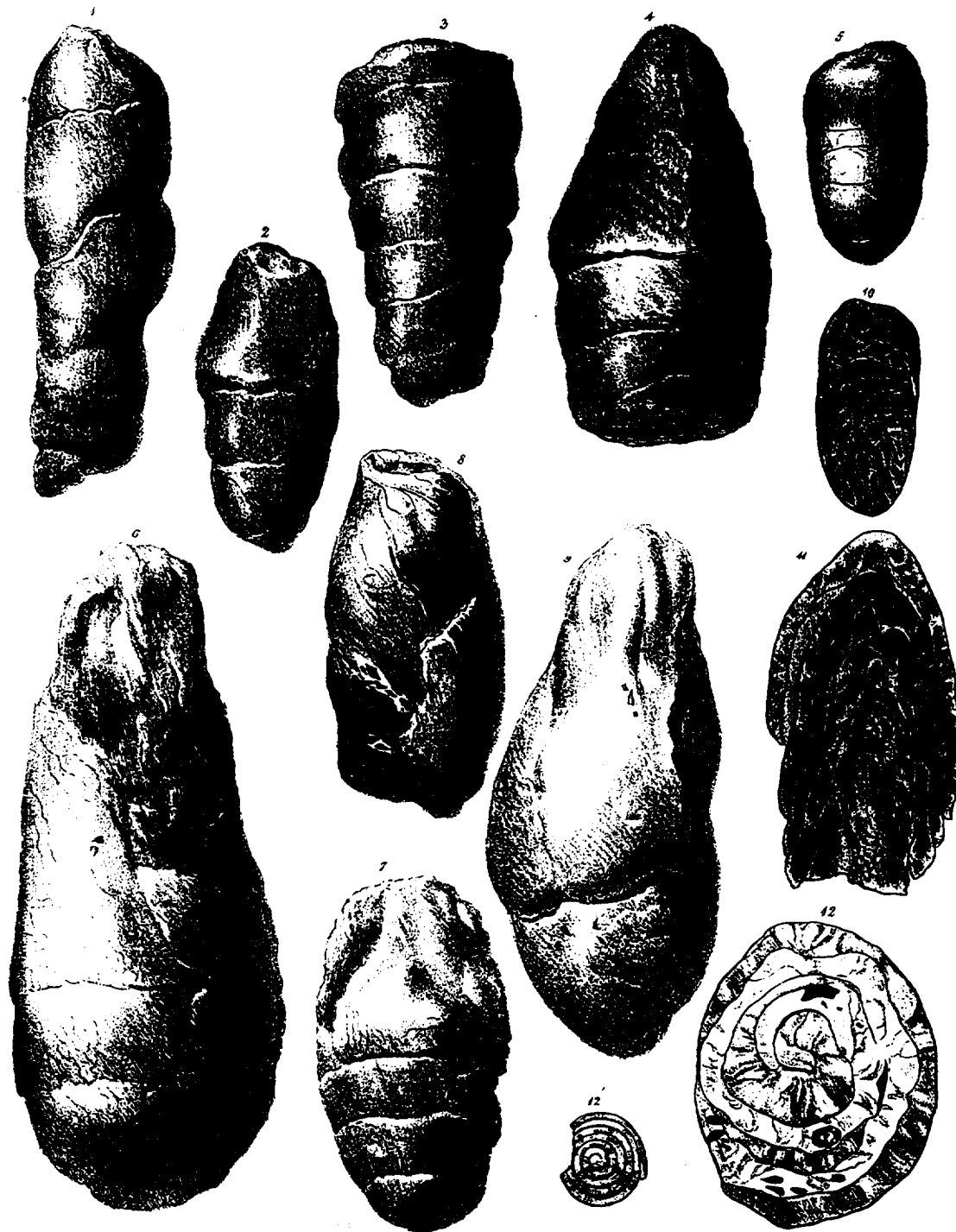
Figure 1—Coprolites and sections of coprolites from the Lias at Lyme Regis, England, approximately $9/10$ths natural size. Reprinted from Buckland (1835) with permission from the Geological Society Publishing House, Bath, United Kingdom.

vertebrate paleontology. Buckland wrote, "Thus in formations of all ages, from the first creation of vertebral animals to the comparatively recent period in which hyaenas accumulated album graecum in their antediluvian dens, we find that the faeces of aquatic or terrestrial carnivorous animals have been preserved" (Buckland, 1835). After Buckland's work, in addition to finding skeletal remains, paleontologists could also identify the end products of feeding activity .

COPROLITE CAVEATS

A wide variety of other fossil feces have been reported since Buckland's early discoveries—including specimens dating from the Ordovician (over 400 million years ago) to the Quaternary (within the last 1.8 million years) Periods. The study and classification of coprolites can be difficult, however, because these trace fossils are highly variable. The first consideration is whether a specimen truly represents ancient fecal material. Fossilized feces are generally identified by shape, so it is quite possible that broken or deformed specimens may not be recognized. At the same time, some inorganic concretions with suspicious shapes may be falsely regarded as coprolites. Although there is no foolproof way of verifying questionable coprolites, it is advisable to correlate a possible specimen (i.e. one with promising morphology) with contents consistent with a fecal origin.

Once a specimen is determined to be coprolitic, other difficulties remain. Unlike skeletal fossils, coprolites do not usually have fixed morphologies or compositions. In most cases, the producer of a coprolite can not be positively identified because the act of defecation separates an animal from its feces. These considerations make it very difficult to draw solid inferences about the feces of specific animals from the study of coprolites. Nevertheless, it is possible to describe the general characteristics of coprolites—i.e. age, size, shape, and contents. These features may provide little information by themselves, but can increase our understanding of the paleoenviroment when correlated with other paleontological and sedimentological clues.

CHARACTERISTICS

Coprolites may be broadly divided into two major types: dessicated and permineralized specimens. The dried dung of Pleistocene sloths, mammoths, and other herbivores has occasionally been preserved in caves or permafrost (Mead and Agenbroad, 1992). These dessicated coprolites look remarkably "fresh", and may provide nearly as much information as recent feces. One researcher identified 72 plant genera in a study of accumulated fossil sloth dung

(Hansen, 1978). Another study isolated a variety of parasites from the same material (Schmidt et al., 1992). Because Pleistocene coprolites were produced by organisms with extant relatives, it has been possible to identify the producers of some of the specimens by correlating droppings with skeletal fossils. This information has subsequently been used to help study Pleistocene megafaunal extinctions as well as feeding habits (Mead and Agenbroad, 1992).

The exceptional "just dropped" quality of Pleistocene dung was preserved under extreme environmental conditions that slowed organic decomposition by microorganisms. Such near-sterile conditions are not stable over geologic time, however. Most coprolites have been fossilized through permineralization—a process in which interstices are infilled with minerals. Lithified (hardened into rock) coprolites retain a three-dimensional configuration, so these specimens can be characterized by external features, including size and shape. The internal composition also serves to differentiate coprolites. Together, these internal and external characteristics may be used to organize permineralized coprolites into broad, non-taxonomic categories.

Coprolites range from less than a millimeter to 34 centimeters on a side (Hantzschel et al, 1968). In general, we assume that the smallest specimens were produced by invertebrates, and the largest deposited by sizable vertebrates. Unfortunately, the correlation between coprolite dimensions and animal size is not absolute. Although the quantity of egested waste is proportional to body size, the entire fecal mass may not be recovered because of the fragmentary nature of fecal material. Feces may be partitioned into smaller units at the time of defecation (as in the deer family) or mechanically broken and separated after deposition. Thus, it is feasible that small masses of fecal material might have been deposited by a large animal. The reverse situation is not possible, however, since a large quantity of fecal material could not have been produced by a small animal at one time. Even so, community latrines from small animals may rapidly build up large masses of accumulated waste such as those found in bat caves or in the vicinity of roosting birds. The bottom line is that coprolite size can be a useful descriptor, but must be interpreted carefully.

When a broad range of coprolites are examined, it is evident that there are several recurring morphologies. Unfortunately, many different species of animals produce feces with similar features, so shape cannot usually be used as a taxonomic character. The one known exception is the spiral morphology recognized by Buckland (Figure 1) and since found in many Paleozoic and Mesozoic localities. Primitive fish (including sharks and lungfish) have a spiral intestinal valve—a primitive character subsequently lost in teleost fish (although a few retain a vestige of this structure) and tetrapods (Romer and Parsons, 1986). This spiral valve is responsible for the coiled configuration of the coprolites,

although there is a debate as to whether the spiral forms actually represent egested fecal material or intestinal contents (Williams, 1972; McAllister, 1985). The assignment of spiral coprolites to primitive fish provides useful paleoecological data, and researchers are attempting to further constrain possible producers by correlation of specimens with faunal assemblages (e.g. Zidek, 1980; Jain, 1983; Gilmore, 1992).

It would be advantageous indeed, if other distinctive coprolite morphologies could be used to identify the taxons of the producers. Unfortunately, cylindrical or pellet shapes, constrictions, pinched ends, and longitudinal striations are all common features of many vertebrate feces, including mammals and reptiles. In a few rare cases, strong evidence points to the probable origin of specific specimens. For example, the locations of coprolites found in the appropriate body cavities of articulated fossil fish suggest that the same fish were responsible for producing the fecal material (eg. Zangerl and Richardson, 1963; Zidek, 1880). Yet, even if a specimen can be positively linked to a given animal, it is possible that another coprolite produced by the same species will look quite different because of variations in diet and conditions of preservation. Nevertheless, recurring sizes and morphologies may be evident when enough specimens are compared.

Despite the transforming effects of diagenesis (geologic change over time), lithified coprolites may still retain recognizable components of an animal's diet. The most common inclusions are biomineralized skeletal elements like bone, teeth, and shell. While many of these constituents may have been damaged by mastication or passage through the digestive tract, others can display sufficient characters to facilitate reasonable identification. Acanthodian ("spiney sharks") scales, ostracods, brachiopods, and ichthyosaur, snake, and rodent bones, are only some of the elements identified in lithified coprolites. If mineralization occurred before extensive microbial degradation, plant tissues may also be preserved. Herbivore coprolites are much less common than carnivore coprolites but petrographic thin sections of some specimens have revealed seeds, stems, and leaf tissue (Chin et al., 1991).

INTERPRETATIONS

After cataloguing the physical properties of coprolites, the question remains: can coprolites provide significant paleobiological information? It might seem that miscellaneous data from anonymous coprolites constitute little more than minor details. Yet, one of the greatest contributions of coprolites may lie in looking beyond the biology of individual animals to the dynamics of the ecosystem. This broader view may be examined by correlating coprolitic data

with other fossils from the area in the context of the depositional environment. If the coprolites are autocthonous (i.e. native to the region), identifiable food residues found in fossil feces verify that the prey animals or browsed plants actually occurred in the environment. Such information may add significantly to the list of known biota from the paleoenvironment, because organisms detected in coprolites may not have been otherwise preserved or recovered.

Perhaps more important than adding to a fossil list, is the fact that coprolitic information indicates trophic interactions. On the simplest level, fossil feces tell us who or what was eaten, but more detailed analyses can refine this information. For example, one researcher (Zidek, 1980) compared the length of coprolites with the sizes of fish scales found inside. Because he had calculated the estimated length of acanthodian fish based on the breadth of their scales, he was able to deduce that the fish that produced a 4.2 cm long coprolite had ingested an acanthodian fish that was at least 25 cm long. This type of information tells us something about both predator and prey, and indicates the types of feeding niches that were occupied in the ecosystem. Continued study of coprolites in paleoenvironmental context should turn up additional ways in which these fossils can be used to augment paleoecological information. It is also possible that coprolites may eventually contribute significant sedimentological and stratigraphic information about certain areas (Hunt et al., 1994). Even so, such insights are dependent on the unbiased collection and study of a sufficient number of specimens.

CONCLUSIONS

Fossilized feces have intrigued researchers since they were first recognized by Buckland over 170 years ago. Many types have been described, including relatively recent, dessicated Pleistocene dung, and older permineralized specimens. Although fresh feces provide a rich source of biological information on extant animals, coprolite analysis is encumbered by two major problems: information loss and anonymity. These difficulties are largely due to the variable nature of feces and to diagenesis over time. This means that care must be taken to prevent overinterpretions of available data. Despite these impediments, coprolites provide a unique record of animal activity that isn't available from skeletal fossils. As such, they may present the best available glimpse into trophic relationships in paleoenvironments.

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The Scientific Romance with Amber

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INTRODUCTION

For at least 10 millenia, a special mystique has surrounded amber. This is probably due to the warmth of its color and touch, its lightness, and the small organisms that are sometimes found in it. Some of the oldest Mesolithic artifacts are amber carvings from Europe, and a rich folklore about origins of amber existed among the ancient Greeks, Assyrians, and Romans. The true origins of amber, as a fossilized resin that bled from trees, was first recognized by the Roman natural historian, Pliny the Elder. By the Renaissance Period, amber was used for elaborate figurines, carved bowls, jewelry, pipes, even caskets. The color of amber, especially in Mediterranean cultures, represented luxury.

Pieces of amber with small organisms in them were particularly sought after, and inspired some rather vivid poetry:

"An ant beneath a poplar found,
An amber tear has covered round;
So she that was in life despised,
In death preserved, is highly prized."
[from the *Epigrams* by Martial]

"I saw a fly within a bead
Of amber clearly buried;
The urn was little, but the room
More rich than Cleopatra's tomb."
[from the *Hesperides* by Pope]

Technical scrutiny can sometimes reduce an object to components that lack any mystique. Not true of amber: electron microscopy and powerful biochemical methods applied to amber (as well as good old field discoveries) have exposed views of the geological past that were unimaginable 50 years ago. Amber is, to quote some clichés from some scientific colleagues of ours, a "unique window to the past, a

"paleontological treasure chest," and a true "time capsule." Science, ironically, has brought more romance to an already unique fossil substance.

AMBER: CHARACTERISTICS AND ORIGINS

As resin bleeds from a tree almost instantly it undergoes chemical changes. Exposure to air and sunlight begins the process of polymerization, or chemical crosslinking, which makes the amber so impervious to degradation. The polymerization takes place primarily with compounds like terpenes, which perhaps evolved to help trees defend themselves against insects that chew leaves and mine wood, and can even prevent fungal attack (terpenes give pine resin its familiar aroma). While the fresh resin streamed out it flowed over debris and small organisms on the trunk, encapsulating them. Small winged insects, spiders -- even tiny lizards and frogs -- wafted into or became mired in the sticky resin, and were entombed. The terpenes render the amber inert and prevent decay of the inclusions, and may also be responsible for remarkable preservation of soft tissues and biomolecules.

Hundreds of deposits of amber occur around the world, even above the Arctic Circle (although none have yet been found in Antarctica). The deposits vary in age from the Carboniferous (ca. 300 million years old [myo]) to ones that are merely hundreds or thousands of years old, such as from New Zealand and East Africa (these are generally referred to as subfossil resin, sometimes as copal). For most deposits, only trace quantities are known. Table 1 indicates the major deposits which have produced hundreds or thousands of insect and other fossil inclusions. There is a popular misconception that all amber is fossilized pine resin; actually, three of the major Tertiary deposits are from extinct species of tropical flowering trees. Oddly enough, too, the botanical origin(s) of the most intensively studied deposits from the Baltic region is controversial. There is good evidence for a pine and an araucarian origin. Araucarians are a primitive type of conifer that appear to have produced most and perhaps all of the Cretaceous ambers; today the family contains only 2 living genera and is restricted to portions of the southern hemisphere.

Virtually all amber is found in water-washed sediments (fresh or marine), where it has been re-deposited. Because the specific gravity of amber is near that of water, it is easily wafted by wave action. In New Jersey and Arkansas, where I have made excavations, the amber is found in thick clays with chunks of black, charcoalified wood. In the Dominican Republic, amber occurs in marine siltstone deposits on steep mountain ridges. Radioisotope dating can routinely be used for rock fossils, but because amber is an amorphous, polymerized organic substance, no credible method for directly dating it has yet been developed: ages must be inferred from the microfossils found in the strata that contain the amber.

TABLE 1 -- Major deposits of fossiliferous ambers.

Location	Age(s)(myo)	Botanical Source(s)
TERTIARY		
Arkansas, USA	40	Dipterocarpaceae?
Baltic Region	15-40	Pinaceae/Araucariaceae
China	40-50	?
Dominican Republic*	25-30	Leguminosae: *Hymenaea*
Mexico	25-30	Leguminosae: *Hymenaea*
Myanmar (Burma)	40	?
Sicily	30	Pinaceae/Araucariaceae
CRETACEOUS		
Canada	70-80	Araucariaceae
France	100	Araucariaceae?
Lebanon	125	Araucariaceae
New Jersey, USA	80-95	Araucariaceae
Siberia	80-100	Araucariaceae?

*Deposits from northern mountains are this age; deposits from eastern mountains are much younger, probably even subfossil resins.

ANCIENT COMMUNITIES REVEALED

Huge quantities of amber are excavated from some areas like the Baltic region and the Dominican Republic. Although we don't know exactly the time scale over which the amber from any one spot was formed (it could have been days, weeks, or years), the quantities suggest catastrophic damage to some ancient amber forests. Perhaps disease or insect outbreaks killed thousands of amber-producing trees or storms, like hurricanes in the Caribbean, wreaked havoc. As the trees became riddled with wood-boring beetles or as their limbs were snapped off by a storm, they exuded thick, long streams of resin. Whatever the reason, without such massive quantities of resin, menageries of insects, plants, and other life would not have become embalmed in amber. Collectively, the inclusions give direct and indirect evidence as to the herbivores, predators, parasites, symbionts, and even some of the flora, in the ancient communities. Ecological inferences would not be possible, too, without the preservation of exquisite, microscopic detail seen in amber inclusions: unlike rock

fossils, even the tiniest and most delicate insects and mites are preserved. I will draw upon Dominican amber inclusions by example.

The most obvious ecological associations in any amber are when one organism is found (rarely) attached to another. Occasionally tiny phoretic mites (hitching a ride) are still found clinging to their host, such as a midge or a beetle. Parasitic nematodes can be found exuded from the abdomen of their host fly; or a parasitic larva partially embedded into its host. My favorite specimen of a symbiotic relationship is in a piece of Dominican amber in the AMNH collection: 7 small white cocoons hang from a twisted spider web; tiny holes show where the tiny adult wasps emerged from their pupal cases (as larvae they must have dined on the spider that spun the web). Of course, there are myriad adult parasitic wasps in Dominican amber. Based on the life histories of their living relatives, we can infer which kinds of insects, also preserved in Dominican amber, they had parasitized.

For some kinds of insects we have an especially good idea of their relationships with other organisms in the Dominican amber community. The stingless honeybee, *Proplebeia dominicana*, is very common (and the only known bee) in Dominican amber. Like stingless honeybees do today, *P. dominicana* harvested resin to construct intricate nests inside tree cavities, and it must have routinely harvested (and often got caught in) resin from the Dominican amber tree. Some bees still have balls of resin attached to their hind legs. The bee even nested, at least sometimes, in the amber tree: in the AMNH is a piece of amber with honeypots from a stingless bee nest (undoubtedly from *P. dominicana*). *Proplebeia* workers sometimes fell prey to stout assassin bugs, also in the amber, which latched on to the bees with tiny balls of resin cemented to their forelegs. We can even tell on what kinds of flowers the extinct bee foraged, by examining the microscopic sculpturing on pollen clinging to the hairs of some bees.

Another major insect player from the Dominican amber forests were wood-boring platypodid and scolytid ("ambrosia") beetles. They, too, are very abundant in the amber (indeed, the most common beetles), and excavated galleries into the wood of the amber tree. Galleries of ambrosia beetles today are lined with material like sawdust, which is composed of chewed wood, frass (insect feces), and fungal hyphae and spores on which the beetles actually feed. Occasionally an amber piece is found where the crumbly galleries had fallen into the resin, along with the beetles and tiny inquiline ("guest") beetles. Pseudoscorpions, tiny tailess counterparts of their namesake, lived with the beetles: ones can even be found still latched onto its host as the beetle flew from the tree!

The general habitat and flora of the Dominican amber forest can be inferred by other kinds of insects. For example, there are weevils and sucking bugs in Dominican amber whose living relatives feed on palms, so palms probably occured in the Dominican
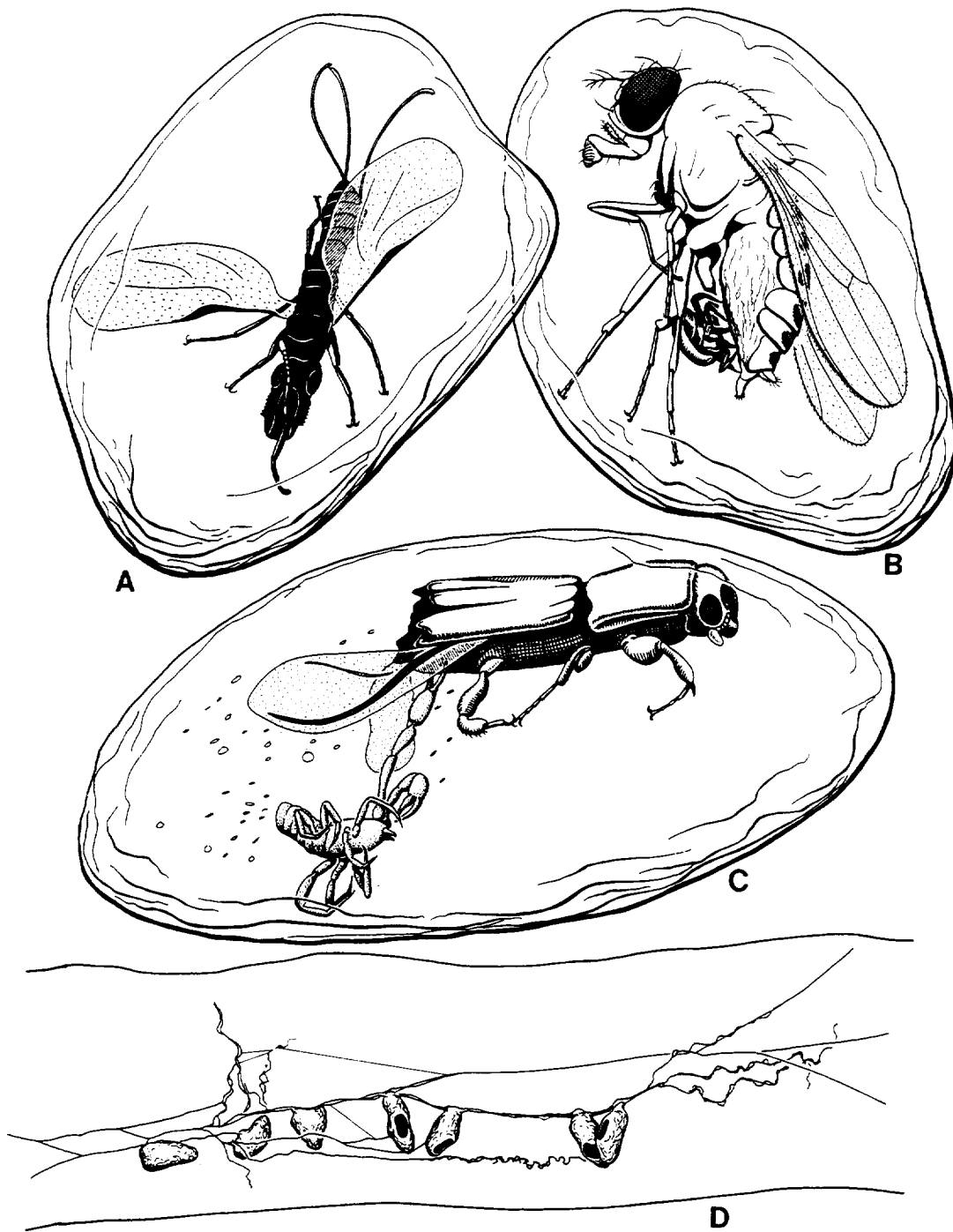
FIGURE 1 -- Examples of biological interactions in Dominican amber (specimens from the American Museum collections). A. A fig wasp (family Agaonidae). B. A fruit fly (family Drosophilidae) with a phoretic mite. C. Bark beetle (family Platypodidae) with a pseudoscorpion attached. D. 7 cocoons of a wasp attached to the web of a spider they had parasitized.

amber forest (although we have no direct proof of this). Likewise, fig wasps attest to the presence of *Ficus* trees -- again with no direct evidence. Myriad other leaf-feeding insects in Dominican amber can probably construct a rather complete flora. There was probably a great deal of dead wood and fungi, given the abundance and diversity in the amber of kinds of beetles, flies, tiny moths, and other arthropods which today are associated with injured trunks and rotting logs.

The evolution of the vertebrate fauna of the Caribbean islands has inspired many zoologists, and greatly perplexed them. Among them were such luminaries as George Gaylord Simpson, who didn't quite know how to explain the apparent lack of land vertebrate fossils older than 20,000 years old (since then, land vertebrate fossils the age of Dominican amber have been found in Cuba, but they are extremely rare). We have in Dominican amber, though, some of the oldest land vertebrates from the Caribbean, and the most complete picture of a vertebrate fauna from that time. Small *Anolis* lizards and tiny *Sphaerodactylus* gekkos are sometimes found in Dominican amber, as is an occasional *Eleuthrodactylus* frog, bird feather, and strands of mammalian hair. The presence of healthy populations of vertebrates is also indicated by various blood-sucking parasites: mosquitoes, ceratopogonid midges ("punkies"), horseflies, phlebotomine midges, fleas, and ticks. The few ticks that have been found are *Amblyomma*. Since this genus feeds on birds and mammals, there was little way to infer on which it fed, until one specimen surfaced containing two hairs with the tick: these ticks fed on mammals. Mammals, birds, and reptiles lived in the Dominican amber forests: we just have not yet found their fossilized bones.

WINDOW TO THE CRETACEOUS

Perhaps the most valuable contributions of amber will come from the study of Cretaceous ambers. When the Cretaceous Period, from 135-65 million years ago, came to end, it brought the extinction of the dinosaurs (excluding their descendants, the birds), ammonites, rudist bivalves, and various other groups. The series of discoveries that eventually led to the finding of a huge crater near the Yucatan Peninsula about 65 myo is one of the most fascinating chapters in paleontology. The impact of a meteor 10 km or so in diameter no doubt had a serious effect on the world climate, perhaps causing conditions like a "nuclear winter." The effect this had, though, on the extinctions of the dinosaurs and other organisms is controversial. It is an enigma why certain groups, like insects, seem to have sailed through the mass extinctions at the end of the Cretaceous. The fossil record of insects in Cretaceous ambers has been very revealing.

The main biological fascination with the Cretaceous Period is that this is when the "flowering" of the world, or radiations of angiosperms, took place (although their origins were probably earlier). It has been fairly standard belief among scientists that
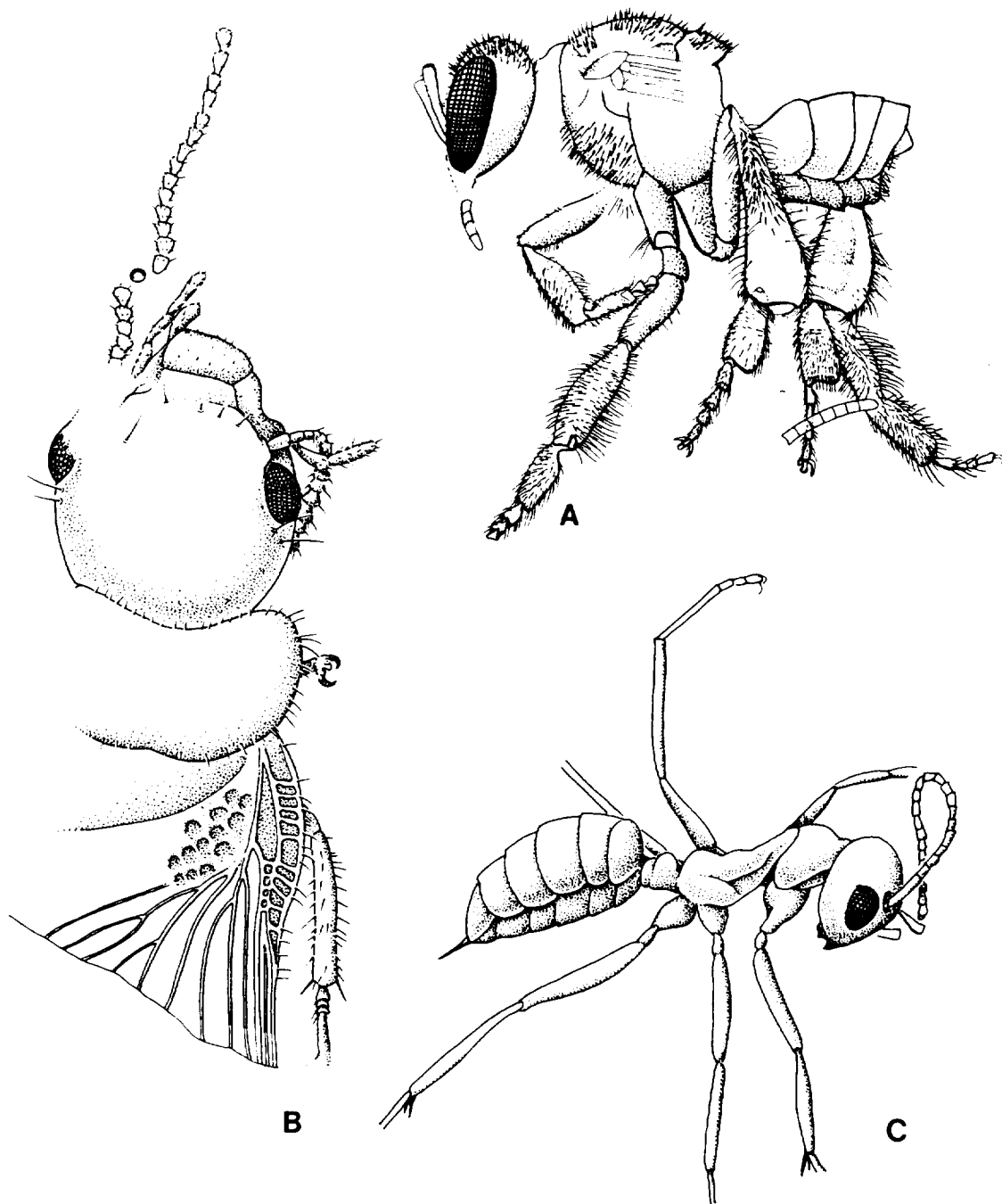
FIGURE 2 -- Oldest known (or near oldest) fossils of ecologically important kinds of
insects, in Cretaceous amber. All are social insects. A. Stingless bee (*Trigona
prisca*), in New Jersey amber. B. Undescribed termite, in Lebanese amber. C.
Ant (*Sphecomyrma freyi*), in New Jersey amber.

the radiations of insects and angiosperms were coupled: the insects feeding on the new array of leaves and wood, flowers, pollen, and nectar; and the plants with an efficient, new way to pollinate. John Sepkoski and Conrad Labandeira recently challenged this thought, by tabulating the earliest occurrences of insect families in the fossil record. They found that the *number* of families of insects was virtually unchanged from the Jurassic to the Cretaceous and, therefore, they concluded, angiosperm radiations had little impact if any on insect diversification. Some large holes exist in this theory.

For one, the fossil record of the Lepidoptera (moths and butterflies) is notoriously poor, as Sepkoski and Labandeira admit, and this probably skews their results severely. The Lepidoptera is the second largest order of insects, with about 130,000 described living species, and one of the most important insect groups in terrestrial ecosystems. With few exceptions, larvae feed on flowering plants, adults on nectar and pollen. The oldest known caterpillar and oldest definitive moth are in Cretaceous amber (a believable moth fossil is in Jurassic rock). All the Cretaceous amber Lepidoptera (not very many!) are quite primitive. This indicates that the Lepidoptera are not much older than the Cretaceous, and certainly radiated sometime during the Cretaceous or early Tertiary (our assurance about the Cretaceous amber Lepidoptera being primitive is greater than for specimens in rock, because the amber preserves such fine details). The same seems to hold true for several other kinds of insects that also are ecological "keystone" groups: the ants (14,000 species worldwide), bees (20,000 species), higher flies (50,000 species), and termites (2,000). For all of these groups, the oldest (or near oldest) definitive fossil is in Cretaceous amber. With the exception of the oldest known bee (an anomalously-advanced stingless bee in New Jersey amber), the other fossils are very primitive compared to most living species -- again, suggesting Cretaceous radiations for these insect groups. I suspect the same will be found for other, very diverse groups of insects, like leaf beetles and weevils, providing that proper studies are done to examine the evolutionary placement of specimens found in Cretaceous amber.

"AMBALMING" AND DNA

The life-like preservation of amber fossils have been best appreciated ever since optics have existed. Early German microscopes revealed on the surfaces of insects in Baltic amber minute pits, grooves, fine hairs, eye facets -- sometimes even color patterns. Near the turn of the century, remains were found of soft tissues in some amber inclusions; although in other inclusions what appears as a solid insect is a husk or cast on the inside. An old Russian study, in fact, reported that, after histologically sectioning and staining leathery tissue taken from an insect in Baltic amber, muscle striations could be seen! Little attention was paid to this study, especially when electron microscopy much later revealed even greater detail in amber-preserved tissues. Both transmission (TEM) and scanning electron microscopy (SEM) have been used:

with the former, organelles in cells can be examined in ultrathin sections 1-2 microns in thickness; SEM is used to examine the surfaces of whole structures.

To exhume an insect in amber, one cannot simply melt the piece: the amber is so polymerized that it just softens at about 360°C and begins to burn, without melting. With a specimen carefully split apart and examined under the SEM, the virtual lack of tissue shrinkage is remarkable. Large flight muscles in an insect thorax retain their living positions, as do tiny muscles in the head and legs. Fine membranes are simply wrinkled; the network of fine air tubules (the tracheae), which delivered oxygen to the tissues, is intact; the brain is hardly changed in size, but the neurones are barely recognizable. Indeed, cellular preservation varies with the kind of tissue: nerve cells preserved poorly; muscle cells preserved with fidelity, even showing the system of fine parallel lines where the actin and myosin protein filaments slide past each other during muscular contractions (oddly, the proteins themselves are probably highly degraded). Mitochondria are organelles where most cellular respiration occurs; they have internal, intricately-folded membranes, the cristae. TEMs of insect flight muscle from amber show numerous fingerprint patterns, which are the cristae. In some small leaves in amber the subepidermal cells were stacked like bricks on end. Modern species of woodboring or ambrosia beetles have sacs beneath the elytra and sclerites, which carry a fungus. It is inoculated into the galleries of a new tree they bore into, and they feed on the "ambrosia" fungus. Ambrosia beetles in Dominican amber have the delicate spores and conidia of the symbiotic fungus still in their sacs.

If the preservation of morphological structures is so remarkable, what about biomolecules? Of course, DNA would be the molecule of choice, being the molecular basis of inheritance. DNA is composed of a string of 4 bases (abbreviated A, T, G, and C) which are repeated in various orders. The sequence of DNA for the same gene (which, say, codes for a particular protein) usually differs between species. These differences are then used to examine evolutionary relationships, or phylogeny.

The study of ancient DNA was virtually unthinkable until the polymerase chain reaction (PCR) was developed. The technique uses an enzyme (taq polymerase) from a bacterium living in hot springs, which amplifies a single DNA strand several thousand-fold. It has been used on 3,000 year old mummies, 12,000 year old sabertooth tiger bones from the La Brea tar pits, and 40,000 year old mammoths locked in ice. A sensation was created when DNA sequences from a chloroplast gene were reported, from 17 million-year-old *Magnolia* and bald cypress leaves, preserved in clays from Clarkia, Idaho! PCR is so sensitive, however, that it can easily amplify contaminants, even under the most exceptional precautions. Some sceptics doubt the authenticity of the Miocene leaf DNA.

Soon after the results on the Clarkia fossils, two studies reported DNA from insects in Dominican amber. One, by our group at the American Museum, examined a

termite; the other, by a California group, examined the common stingless bee in this amber. The termite is *Mastotermes electrodominicus*; the genus has 20-40 myo fossils from the northern hemisphere, but today the group is relict: only one species is living, in Australia (oddly enough, it is a serious pest). DNA analysis of the extinct termite addressed two evolutionary questions. One: Is the genus *Mastotermes* a natural grouping? It is traditionally defined by a large, fan-like lobe at the base of the hind wings, many wing veins, and a pronotal plate on the thorax larger than in other termites. But, cockroaches have these features too, and so they evolved well before *Mastotermes*. Perhaps with DNA we could have more characters to compare, where the morphology alone was not conclusive. Second: roaches, praying mantises, and termites are usually placed in a group called the Dictyoptera; what is the relationship of *Mastotermes* to these subgroups? *Mastotermes* is social and has castes like other termites, but is unique by laying its eggs in clumps, like a rudimentary roach egg sac.

The 18S rDNA gene was sequenced, because this gene has been studied in many kinds of insects (the 18S refers to its size; r refers to ribosome, the organelle that produces proteins). Two fragments comprising about 400 bases were sequenced. The analyses revealed that the extinct *Mastotermes* is a true termite even though it retains features of a distant roach ancestry. And, the genus is monophyletic; that is, the living and extinct species share a closer relationship with each other than with any other termites. Analyzing the DNA phylogenetically is not only the goal of the study, but also a test of the authenticity of the DNA sample: if it's too divergent, or exactly the same as one of the living sequences, it is likely to be a contaminant.

Since our report on the termite, five other amber organisms have had DNA sequenced. In Dominican amber: a *Hymenaea* leaf, a woodgnat (family Anisopodidae), fruit fly, and beetle (family Chrysomelidae). DNA has also been reported from a weevil in 125 million-year-old amber from Lebanon (curiously, this result was published on the day the movie version of "Jurassic Park" was released). We can't stress enough that examining evolutionary relationships are our *raison d'être* for studying ancient DNA, not simply "going for the old," and certainly not to clone extinct organisms (consider this: the day cloning an extinct animal becomes possible is also the day humans become immortal).

There is little doubt that amber preserves DNA much more consistently than any other kind of fossil. Why? We know that chemical differences in ambers affect preservation (Dominican amber preserves better than Baltic), but probably all ambers preserve so well because of terpenes and terpenoid precursors. These are volatile organic compounds in the resin: they have antibiotic properties which would prevent decomposition and, perhaps, are responsible for fixing and dehydrating tissues. Dehydration is essential to preserving DNA, but such little tissue shrinkage must be due to fixation, perhaps by the terpenes rapidly replacing the water in soft, internal tissues. Experiments are currently underway to determine the chemical basis of how
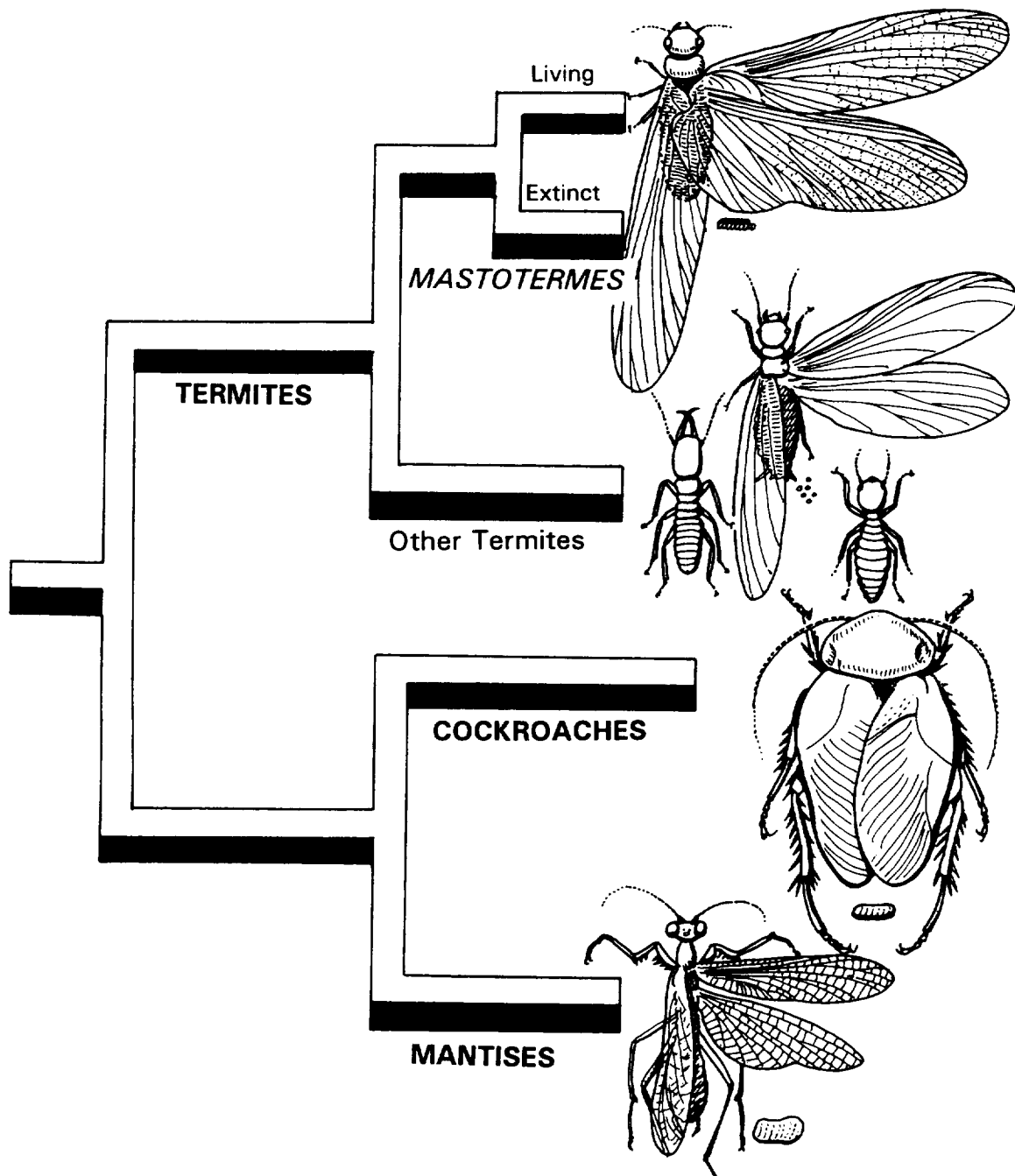
FIGURE 3 -- Phylogeny of the "Dictyoptera" based on living and extinct DNA. The extinct DNA is from a 25-30 million-year-old termite in Dominican amber, *Mastotermes electrodominicus*.

resins embalm tiny organisms so well, which is a process so distinctive we prefer to coin it "ambalming."

IS THERE "STILL LIFE" IN AMBER?

If amber preserves such delicate biomolecules as DNA (though not perfectly), does it preserve living organisms? Complex eukaryotes like insect mummies are incompletely preserved; but can amber actually preserve entire, reproducible viruses, bacterial and fungal spores, and pollen? For example, pollen has a hard outer coat (the exine) that can remain intact for millions of years in sediment. It also can remain dormant for years in some cases, especially in dry conditions. Because amber has dehydration-like properties, it is plausible that amber could could preserve viable pollen grains. Elizabeth Bonwich, an intern student at the American Museum, did some simple tests to examine viability of pollen from the extinct species of Dominican *Hymenaea* amber tree. Entire stamens from the flowers of the extinct *Hymenaea* are fairly common in Dominican amber, so the anthers of several specimens were split open and the material inside was spread onto medium in petri dishes. One medium would stain blue around pollen grains in the presence of active enzymes; another would allow the microscopic pollen tube filaments to grow. Both are good tests of viability. Not surprisingly, viable pollen was not found. IF viable pollen from the extinct species was found, then it could be used to pollinate flowers of *Hymenaea verrucosa* or *H. coubaril*, which are close living relatives. A perfect duplication of the extinct species couldn't be made this way, but the hybrid would approximate certain non-fossilized features of the extinct tree, such as its growth form and the kind of seed pods it had (besides the flowers, its leaves are preserved in Dominican amber).

Several factors have made the effort of resurrecting viruses and bacteria from amber an intensive one. Bacterial genomes consist of a single molecule of DNA not complexed with labile histone proteins (as in eukaryote chromosomes). Also, some bacteria, like the nitrogen-fixing soil bacteria in the genus *Azotobacter*, form dormant, thick-walled cysts that are very resistant to desiccation, radiation, and even physical damage. With such simple genomes and enduring dormant stages, finding viable bacteria in amber is much more likely than finding any kind of viable eukaryotic tissue or cell. However, it too is not without monumental difficulties and even serious ethical concerns.

There have been three *possible* successes of bacterial isolation from amber thus far. The first was done by Howard Ochman and Alan Wilson at the University of California, Berkeley. Bacterial cultures that were plated out of Dominican amber were then sequenced for their DNA (the modern method of identifying bacterial species). It was an unidentifiable species. Most recently, two researchers in California and Japan have independently isolated *Bacillus* species, one from the extinct Dominican amber

stingless bee, and the other from bubbles in Baltic amber. Scrupulously sterile conditions are required to rid the fine surface cracks on a piece of amber of its modern, contaminant bacteria. But, the fatal caveat of ancient bacterial research is that it is virtually impossible, at present, to recognize an extinct bacterium from an extant, newly discovered species. For perhaps no other group of organisms is the modern fauna of bacteria so poorly known. One study found that a gram of average forest soil contains thousands of kinds of bacteria, only a fraction of which are known to science!

Ethical concerns over resurrecting possible pathogenic, extinct microorganisms are certainly justified. For some microorganisms in amber, a pathogenic past could easily be inferred. We can certainly expect the ambrosia fungus in the mycangia of wood boring beetles in amber to have killed trees (the fungus and their insect vectors perhaps even caused or contributed to the demise of the amber trees themselves). Isolating viable spores of ambrosia fungus from amber would (or should) be a very controversial project. Extraction and culture of bacteria and viruses from amber, however, is a hit-and-miss approach. No precautions are made to screen out potentially pathogenic species and, in fact, there is little means to predict pathogenicity. Concern extends not just to whole bacteria cultured from amber, but to current efforts in at least one lab to suture the fragmented DNA from a possibly extinct bacterium into the genome of a close living relative. In the worst scenario a unique pathogenic feature would unwittingly be infused into a living species of bacteria; at best, a mosaic microbe would be produced, and, given how morphologically featureless bacteria are, the scientific value of that is questionable. The ethics of working with DNA from amber was enough to divert the research of one Japanese scientist: after he had isolated part of a gene controlling development in a fruit fly in amber, his university prevented him from inserting the extinct DNA into an embryo of a living fly.

CONCLUSIONS

Science progresses by the testing of ideas. This applies particularly to the study of the remarkable fossils in amber, whether it is tissue preservation, DNA, or microbial viability. An obsession with technological feats makes us into mere tinkerers, and distances us from social and scientific ethics. Of current concern is the safety of rare amber fossils, even in museum collections, which might be sacrificed (even partially) for destructive analysis. Considerable thought and experience with amber fossils must dictate responsible stewardship of these collections.

ACKNOWLEDGMENTS

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Will the Dinosaurs Rise Again?

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INTRODUCTION

The movie Jurassic Park has engendered much excitement and some speculation among both the general public and the scientific community as to the possibilities of genetic research and molecular preservation.

But will the dinosaurs "rise" again? Will scientists be able to 'clone' a dinosaur out of bits of genetic material and once again unleash these great beasts to walk the earth? If it is possible, should it be attempted? If not, why are time, money and effort being expended by several groups of investigators in attempts to isolate and characterize the DNA of these extinct creatures, if such DNA can possibly still exist? What can we hope to learn from these efforts, should they be fruitful?

We will examine the following issues dealing with this line of study:
1. Information to be gained from the study of DNA;
2. Strategies of analysis: new technologies and techniques;
3. Selections of gene sequences for analysis;
4. Preservation potential of biomolecules;
5. Role of protein or amino acid analysis;
6. Sources of ancient DNA;
7. Problems of working with "extinct" DNA;
8. Obstacles to the resurrection of extinct animals;
9. Brief review of current progress.

INFORMATION TO BE GAINED FROM THE STUDY OF DNA

DNA, or deoxyribonucleic acid, is the molecule which carries all of the information —or the molecular blueprint — needed to specify an organism, from bacteria to human. Height, gender, and hair color, as well as the size of red blood cells, metabolic pathways, and the ability to utilize sugar and other nutrients, is delineated in the specific order of nitrogenous bases, aligned on a sugar-phosphate "backbone". The base sequences make up genes, which interact with other genes or act alone to establish all the traits of any organism. Genes are contained on chromosomes, which (in eukaryotes) are found within the nucleus of cells. This genetic information is in every cell that is part of that organism. In theory, then, one should be able to take a skin cell, liver cell, or any other nucleated cell, and grow a being which is genetically identical to the donor, hence the premise of the movie. Technology, however, has not yet progressed to the point that today's scientists

can accomplish this feat even with living animals. Clearly, then, we are currently far removed from accomplishing the feat of bringing extinct organisms back to life.

Much can be learned, however, from bits and pieces of DNA that may be preserved in "fossil" organic remains. From the standpoint of a paleontologist or evolutionary biologist, the most important of these is **relationships** (Figure 1).
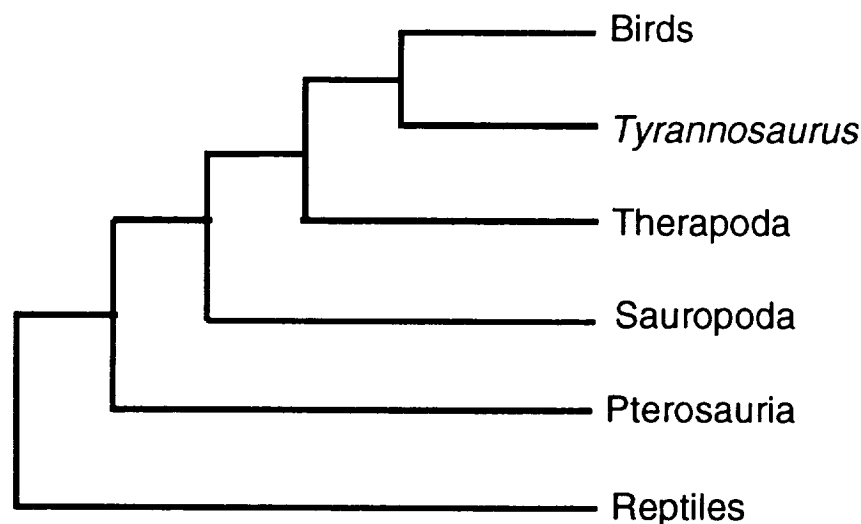

Figure 1. Hypothetical relationship between reptiles, birds, and *Tyrannosaurus*

In living animals, comparison of selected DNA sequences allows for the determination of closeness of relationships, proximity of shared common ancestors, and the ability to estimate, at least tentatively, the time of divergence of lineages. In most cases, the molecular data thus obtained verifies and substantiates estimates based on comparisons of shared derived characters, or morphometric analysis. Occasionally, however, molecular evidence will show that an organism is more closely related to a branch whose other traits place it in a different position (Bahl and Smith, 1965; Dayhoff and Eck, 1968; Eernisse, 1983; Ambler and Daniel, 1991).

Working with extinct organisms poses different problems. Much of what we know about these organisms comes from traits that are not preserved in the fossil record. Mating strategies, sexual dimorphism, gestational rates, feeding behaviors, coloration and other soft tissue characteristics may be derived traits which directly influence placement in phylogenetic analysis. Sample size and incompleteness of specimens also present problems in phylogenetic analysis of fossilized organisms. Because of the biases in the fossil record, there are generally few samples upon which to base such analyses, and quite often placement of taxa is based upon the traits of single bones, or teeth.

Until recently, morphological analysis based on skeletal remains was the only tool available for scientists to determine proximity of sister groups as well as ancestor-descendant relationships for extinct fossil organisms. The proposed lineages for dinosaurs as a group are based on careful analysis of the traits which are revealed in the bones and other "hard" parts preserved in the fossil record. Much information is contained in the characteristics of the bones, and by comparing micro- and macrostructures with those of living animals, many traits of dinosaurs have been inferred (Reid, 1984a, 1984b; 1985; deRiqles,1980, 1983; Chinsamy,1991; Varrichio, 1992). Much information is also lost in

the decay of soft tissues and cells, which would carry biochemical information, internal organization, and perhaps indications of thermoregulatory capacities.

If it can be shown, however, that DNA or other biomolecules can be preserved — at least in small pieces — in the remains of extinct organisms, then this information may not be lost after all. By targeting specific gene sequences, it may be possible to deduce biochemical characteristics. For example, if parts of the hemoglobin gene can be reproduced, perhaps we could estimate the configurations of this vital protein (Perutz, 1983). By comparisons with hemoglobins of extant organisms, estimates of oxygen carrying capacities could be made (Braunitzer and Hiebl, 1988, Caruso, et. al. 1991, Islam, et. al, 1990). The hemoglobin gene would also hold information as to the thermoregulatory mechanisms of these animals, potentially solving unambiguously the "warm-blooded/cold-blooded" debate (Rodewald, et. al., 1987).

Also, through comparative studies of sequences from various extant taxa, it is possible to estimate the extent of evolutionary divergence (Kocher, et al, 1989, Van de Peer, et al., 1990, Naito, et. al, 1991). Base-pair substitutions accumulate over time within a species genome. By comparing the amount and type of these changes, one cold estimate how quickly some DNA "evolves" relative to other segments, or which bases or genes have the most flexibility or are more conserved over time. To be able to isolate DNA directly from extinct, and presumably ancestral lineages, would allow the direct verification of currently extrapolated conclusions, and give concrete validation to such estimates as rate of changes, and direction or polarity in base pair changes (de Queiroz, 1985, Eernisse and Kluge, 1993).

The compilation of these data would yield much understanding of the physiology of extinct creatures, including dinosaurs, that is not attainable through other methods. Also, it would provide a much clearer picture of genetic change over time, and the mechanics behind "evolution."

STRATEGIES OF ANALYSIS

The explosion in the field of biotechnology has made areas of study available to paleontology that were never before possible. In terms of the analysis of DNA, the single most important technology is the polymerase chain reaction. This technique uses very small amounts of DNA (as little as one molecule) as a template from which to artificially synthesize numerous, new, identical molecules. Certain known regions of a gene are targeted by specifically designed oligonucleotide primer molecules. These primers anneal with, or stick to, complementary regions on the target molecule, and represent starting points for the synthesis of new DNA molecules by enzymes called DNA polymerases. Through repeated cycles of heating and cooling, DNA synthesis continues until a high concentration of DNA (more than 1 million copies of the original template) is attained. This exponential amplification produces enough copies of the target strand of DNA to be manipulated and analyzed through standard molecular techniques, such as cloning and enzymatically directed sequencing (Sanger et al., 1965). Coupled with new and refined techniques for extraction of biomolecules tightly adhered to matrices, this technology has become a powerful tool for analysis.

Analytical software is available (e.g., CLUSTAL, FASTA, GDE, etc.) which allows the sequences obtained by the above methods to be matched against homologous sequences from other species which have been entered into a data bank. Statistical analyses can then be performed and estimates of relatedness and genetic distance can be obtained. Phylogenetic trees based on sequence data can be constructed, using software packages such as PAUP and PHYLIP. This allows for the objective placement of an organism within

the framework of known taxa. It also allows any modern DNA that may be contaminating ancient tissues to be characterized and possibly recognized.

New technologies, or improvements in the sensitivity of old ones, could allow for the recognition of other biomolecules which may be preserved in fossils. For example, High Performance Liquid Chromatography (HPLC) is a very sensitive method that allows organic components such as proteins, amino acids, DNA, RNA, lipids, or polysaccharides to be separated and identified. Two other separation methods, gas chromatography and infrared spectroscopy, are also extremely sensitive in detecting minute amounts of organic compounds in fossil bones.

Electron microscopy, coupled with electron probe capabilities, allows not only for very detailed analysis of microstructural preservation of fossil bone, but also for the identification and localization of DNA molecules or certain amino acids, when these molecules are tagged with probes labelled with gold or other electron dense elements (Bianco, et. al, 1985).

SELECTIONS OF GENE SEQUENCES FOR ANALYSIS OF EXTINCT DNA

When working with DNA purportedly obtained from extinct organisms the selection of gene sequences for amplification and/or analysis is a crucial step. In the case of dinosaurs, for which there is no direct living representative, the genomes of the closest living relatives (based on morphological analysis) are examined for conserved sequences. Archosaurs, such as alligators and crocodiles, are believed to have shared a common ancestor with the Dinosauria, and members of Aves (birds) are believed to be their descendants. When selected regions of genes for these taxa are compared, homologous sequences can be identified. Regions of homology, where at least 15 bases are identical between the two groups, are good places to start when designing primer molecules. The rationale is that if there is so little change between these two groups currently, then the dinosaurs, which theoretically fall somewhere in between these two lineages, would also contain the same sequence within their genomes.

The chances for successful amplification are increased if the target gene sequence is present in multiple copies within each cell. Nuclear DNA sequences of ribosomal constituents, such as 18s and 28s rDNA, are often used in such studies. Mitochondrial DNA sequences are also good candidates because not only are there several to thousands of mitochondria per cell, but the complete mitochondrial genome has been sequenced for many taxa and has been entered into data banks, and are available for comparative studies. However, association with histone proteins, which may provide some protection against degradation, does not occur in mitochondrial DNA. Therefore, these targets may not be as ideal as nuclear or genomic sequences for studying extremely ancient materials, such as dinosaur remains.

For phylogenetic significance, it is desirable that the selected homologous primer sequences for known taxa flank regions of relatively high variability. This allows for better definition of phylogenetic placement than if there are relatively few changes across a broad range of taxa. Also, it is easier to tell if there is contamination with modern DNA. If DNA from ancient samples can be obtained and amplified, then analysis can reveal if any base pair changes in the sequences from ancient materials are intermediate between the modern taxa being used for comparison.

PRESERVATION POTENTIAL OF BIOMOLECULES

It is a commonly held belief, based on experimental evidence as well as extrapolated predictions based on studies of DNA in aqueous solution, that nucleic acids do not survive in fossil remains on a geological time scale (Lindahl, 1992). These assumptions, however, are being challenged by researchers who are continually pushing back the age for identification and recovery of DNA and proteins obtained from fossils preserved under rare and specific conditions (Pääbo, 1985, 1989a; Pääbo, et al, 1989; Hagelberg and Clegg, 1991, 1992; Higuchi and Wilson, 1984; Higuchi, et. al, 1984; Golenberg, et. al, 1990; DeSalle, et. al, 1992; Cano, et. al, 1992 a, b, 1993; Muyzer, et al, 1992; Collins, et. al, 1991a, 1991b; de Jong, et. al, 1974; Gurley, et. al., 1991).

The double stranded, helical structure of DNA is more resistant to damage than single stranded RNA (Lindahl, 1992), but its structure and chemistry make it susceptible to certain types of damage over time. Conversion of bases through hydrolytic deamination (guanine changes to xanthine, cytosine to uracil or its derivatives) and depurination (removal of the bases guanine and adenine from the sugar-phosphate backbone) affect the informational content of the molecule. Exposure to oxygen free radicals or UV radiation also damages DNA strands (Eglington and Logan, 1991). In a living organism, strategies have been developed to repair such DNA damage as it occurs, maintaining genetic information, and preventing accumulation of errors (Grossman, 1991). With the death of the organism, this self-repair process stops, while enzymatic attack and exposure to water, oxygen, and ultraviolet radiation continue with advancing decay. There are rare cases, however, where DNA is protected from such damage.

Exposure to water is probably the single most destructive force acting on the DNA molecule. Water has been shown to initiate strand breaks by attacking the base-sugar bonds. Where the base is lost, the chain is weakened, and eventually cleaved (Lindahl, 1992; Eglington and Logan, 1991). Given these facts, a crucial step in the preservation of DNA is relatively rapid dehydration of tissues. One way that this occurs is through entrapment of organisms in amber-forming resins.

Amber is an amorphous polymeric glass, with mechanical, dielectric, and thermal features common to other synthetic polymers (Wert and Miller, 1988). It originates from the resin of woody plants, and is commonly recognized as sticky odoriferous "pitch." Natural resins are complex mixtures of terpenoid compounds, acids, alcohols, and saccharides secreted from parenchymal cells, some of which have preservative and antimicrobial properties (Langenheim, 1990; Poinar and Hess, 1985b). Resins are not restricted to the conifers but occur in a wide range of flowering plants (Langenheim, 1990); Through the aging processes of oxidation and polymerization, the resin becomes harder and ultimately forms the gemstone known as amber. The preservative properties of amber make it a suitable source of tissue with extractable DNA, from which genetic studies can be conducted (Cano et al., 1992a, 1992b, 1993; DeSalle et al., 1992, Poinar et. al., 1993).

What makes amber such a good preservative of DNA? Studies conducted on the trunk resin of the tree *Agathis australis* may provide part of the answer. First, the sugars arabinose, galactose, and sucrose are present in such resins. High concentrations of these sugars in the resin would make the resin hyperosmotic to the cell, drawing water out and achieving tissue dehydration. Under water-free conditions, biochemical reactions, including those involved in the degradation of nucleic acids and proteins, are inhibited. Microbial activity which results in the degradation of cellular components is also halted, as there is not sufficient water to carry out microbial metabolism. Second, alcohols such as fenehyl and communol and terpenes such as alpha-pinine, limonene and dipentene may act as fixatives to preserve tissue. Evidence of such preservative properties can be seen in the electron photomicrographs of Poinar and Hess (1985b) in which they show evidence of chromatin, endoplasmic reticulum, and mitochondria of a 40 million years before present

(mybp) midge fly in Baltic amber (Figure 2). Additionally, one of the oxygenated derivatives of terpene hydrocarbons is aldehyde, which may also serve as a fixative of embedded tissue.

Effective dehydration can also occur with the removal of DNA from solution. This process occurs through adsorption of DNA onto mineral surfaces (Romanowski, et.al, 1991). Hydroxyapatite is known to have a very strong binding affinity for DNA (Adegoke, et. al, 1991; Johnson, et. al., 1985) and this component is, of course, the mineral which predominates in bone. Removal from solution through adsorption protects the molecule from attack by hydronium ions.
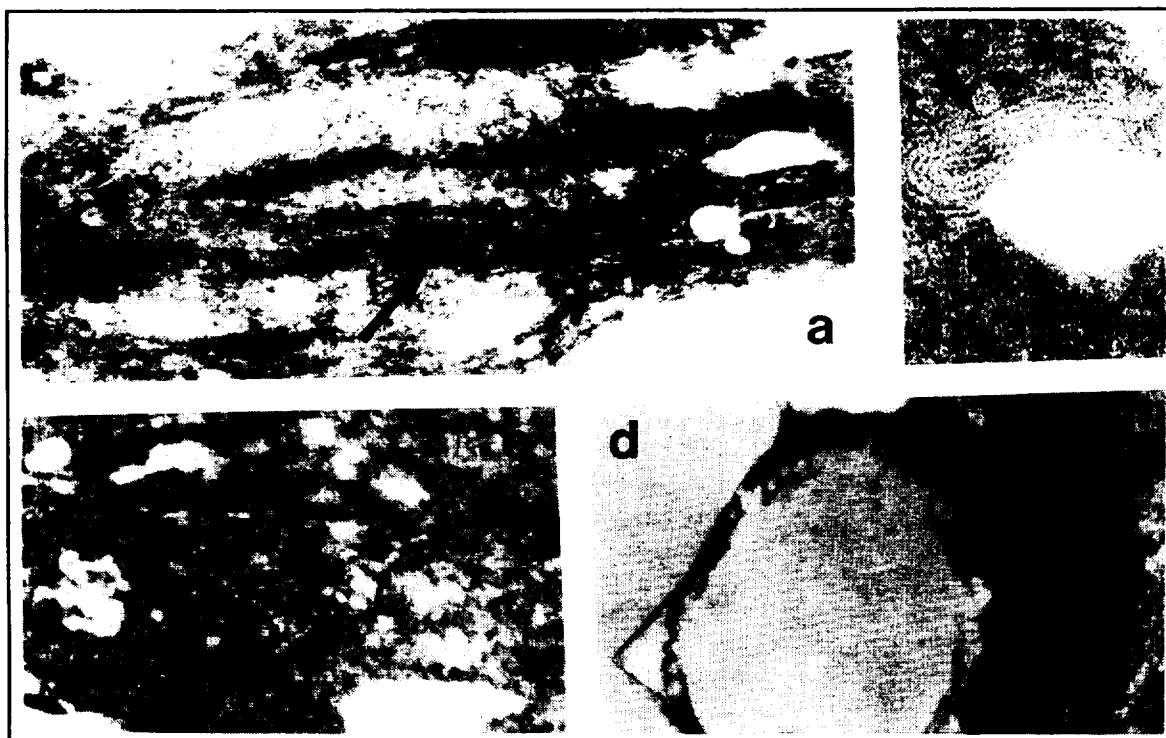
Figure 2. Electron photomicrographs of tissues from amber-entombed insects exhibiting various structures and organelles. (a) mitochondrion; (b) endoplasmic reticulum; (c) chromatin; (d) muscle tissue. *Courtesy of Dr. George O. Poinar, Jr.*

Another consideration in the long-term preservation of DNA is the pH of the environment. Acidic environments may increase the rate of degradation of this molecule as H+ ions can attack the OH groups of the sugars and the nitrogenous bases, contributing to strand breakage. Bone also sets up an alkaline environment (hydroxyapatite is a basic compound), which can favor the preservation of DNA. However, Lindahl (1993) claims that in the vicinity of 7.4, variations in pH do not seem to be a major factor in the degradation of DNA

Oxidation is another source of DNA damage, and removing DNA from water as in amber or bone does not protect the molecule from oxidative attack. Oxygen, in its molecular state, does not attack DNA, but rather it is the formation of oxygen free radicals which attack the nitrogenous bases. Oxidative attack would be rapid at first, but then would level off (Pääbo, 1989). It is proposed that chelation of copper or other metal ions

(Romanowski, et. al., 1991, Eglington and Logan, 1991) enhances the preservation of this molecule by contributing to a reducing environment, and compensating for the production of oxygen free radicals

Exposure to ultraviolet light also causes extensive damage and degradation of DNA, and rapid burial of an organism is important to minimize the consequences of UV damage to DNA. Rapid burial is implied in the preservation of fossils such as dinosaur bones. It is assumed that predation, bloat, bacterial decay, scavenging, and other taphonomic processes seen today were equally active in the Cretaceous in the breakdown of organic remains. To avoid total disintegration of remains by these forces, burial must have occurred relatively soon after death. This is particularly true when skeletons are found fully articulated. The assumption is made that burial occurred before the soft tissues like ligaments, muscles, and skin, which hold the bones together, had undergone complete decay.

ROLE OF PROTEINS AND AMINO ACIDS IN ANALYSIS OF FOSSIL MATERIAL

Like DNA, proteins contain much phylogenetic information in the sequences of their amino acid constituents. Phylogenetic trees have been constructed for many organisms based upon protein sequence comparisons (Dayhoff and Eck, 1968, Romero-Herrera et al, 1978, 1982, Joysey, 1988).

To some degree, the conditions for the preservation of proteins is linked to those for DNA preservation. Some believe that even if DNA is completely degraded and non-recognizable in fossil material, proteins may survive because of protection obtained from their complex tertiary and quaternary structures (Eglington and Logan, 1991).

There is a considerable body of evidence that enough components of original proteins remain in some fossil materials to cause positive immunological reactions to probe molecules (Muyzer, et al, 1992a, 1992b; Armstrong, et al, 1983, Lowenstein, 1981, Collins, et al. 1991).

Beyond the phylogenetic information contained in protein constituents, it is possible that remnants of these molecules may provide a means for "dating" fossil remains, by analyzing the "handedness", or shape of the constituent amino acids. In living organisms, the 20 amino acids which comprise all proteins exist in the L configuration (Bada, 1991, Eglington and Logan, 1991). However, upon death of the animal, conformational changes in the shape of the amino acids to the D form (a process known as racemization) occurs spontaneously until equilibrium is reached. This process, however, is modified or slowed by environmental conditions such as dehydration, protection from high temperatures, and association with mineral matrices. Racemization rates differ for each of the amino acids, with isoleucine being slower than any of the other amino acids to racemize (Bada, 1991). Studies of the degree of racemization occurring in amino acids isolated from fossil remains, then, is a good indicator of the state of preservation of that fossil material.

Dating of the molecular components isolated from fossil material can also be done through analysis of isotopes; specifically the ratio of 13C to 12 C, or 15N to 14 N (Macko and Engel, 1991; Weiner, et al., 1976).

Protein and amino acid information also can be used as a corollary to DNA data. Because the conditions for preservation of protein components mirror those of DNA preservation (that is, dehydration, protection from exposure to high heat, UV radiation and oxidation), protein analysis can be a good predictor of the potential success of DNA analytical attempts. If amino acid constituents of proteins can be identified in fossil remains, and if racemization is less than what would be predicted from the age of the fossil, then conditions were favorable for the preservation of proteins, and possibly, DNA. This has been shown to be the case for materials imbedded in amber (Wang and Bada, 1994) where no apparent racemization of amino acids is seen.

SOURCES OF ANCIENT DNA

There is already a body of scientific evidence which supports the use of DNA from extinct animals and plants for phylogenetic studies. Poinar and Hess (1985a) reported ultrastructural evidence indicating that 40-million year old Baltic amber contained partially preserved insect tissue, including nuclei, mitochondria, muscle fibers, and endoplasmic reticulum. Higuchi and coworkers (1984a, 1984b) demonstrated that remains of a mammoth and the extinct species, the quagga, contained fragments of the original DNA. Pääbo (1985, 1989) reported the extraction of clonable DNA from the 2,400 year old mummy of a child. Subsequent DNA analysis revealed fragments measuring approximately 3.4 kilobase pairs. Thomas, et al, (1989) isolated DNA from hair found in century old untanned hide and a piece of dried muscle collected from an extinct marsupial wolf. This DNA was later enzymatically amplified by PCR and phylogenetic studies were made.

More recently, Golenberg, et al. (1990) isolated and analyzed *Magnolia* chloroplast DNA from a Miocene *Clarkia* deposit dated 17-20 millions years old. Cano, et. al., (1992a, 1992b) isolated and characterized DNA from the extinct bee *Proplebeia dominicana* in 25-40 million year old Dominican amber. DeSalle, et. al.. (1992) employed DNA extracted from fossil termites to resolve phylogenetic relationships between the termites, cockroaches, and mantids. Cano, et. al. (1993) extracted DNA from a 120-135 million year old nemonychid weevil (*Libanorhinus succinus*) in Lebanese amber and showed by nucleotide sequence alignments and phylogenetic inference analyses that the fossil weevil was most closely related to the living (extant) nemonychid weevil *Lecontellus pinicola*. Finally, Poinar, et al., (1993) used DNA sequences from the extinct legume *Hymenaea protera* in Dominican amber in a biogeographical study in which they showed that the extinct *H. protera* was most closely related to the extant African species *H. verrucosa*, a conclusion which is also suggested by morphological studies.

Amber, the "golden gem of the ages," is highly sought after for its beauty and color, as well as for its biological properties. This gemstone represents an important repository of paleontological and evolutionary information. The preservative properties of amber have already been noted earlier in this paper. These properties make biological inclusions in amber a natural source for the study of ancient DNA. A plethora of biological information is waiting to be discovered in this hardened tree sap known as amber or *Bernstein* (burning stone).

The systematic study of biological inclusions in amber began in the 1830s when 64 genera of plants, 174 species of flies, ants, beetles, and moths, 73 species of spiders, and many species of centipedes were described by Runge, Berendt, Menge, Geopper, and others (See Bachofen-Echt, 1949). Since then, amber has been used to study morphological relationships among various species of animals and plants (Poinar, 1992).

The oldest verifiable DNA has come from amber inclusions (Cano, et al., 1992a, 1992b, DeSalle, 1992, Cano et al., 1993, and Poinar et al, 1993). Empirical data inferred from amino acid analyses of a 40 mybp fly in Baltic amber, supports the longevity of biological tissues in amber. These studies, conducted by Xueyun Wang and Bada (1994) showed that the half-life of aspartic acid racemization in the fly tissue is $>3 \times 10^8$ years and that the rate of racemization of this amino acid is generally comparable to the rate of depurination of nucleotides. These results showed that the amino acids obtained from the fly tissues are the most ancient, unaltered amino acids found thus far on earth,and also that DNA is likewise well preserved in amber-forming resins. They attribute the high degree of preservation of these biomolecules to the state of dehydration in which these molecules are found.

Experimental studies in the laboratory of Dr. R. Cano also suggest that DNA molecules exposed to accelerated weathering, including exposure to UV light, high humidity, and elevated temperatures (40-50 °C) remain intact after 30 days of such

treatment when immersed in *Araucaria* resins, whereas after similar exposure in an aqueous environment are completely degraded (R. Cano, personal communication).

Preliminary analyses of dinosaur bones from the Hell Creek formation also show potential for DNA preservation. Trabecular bone taken from the marrow cavities of an exceptionally well preserved, articulated *Tyrannosaurus rex* skeleton show little evidence of diagenesis (rearrangement of component minerals to form a new product), and indeed this bone is comparable in texture and appearance to modern bone which has undergone desiccation (Figure 3).
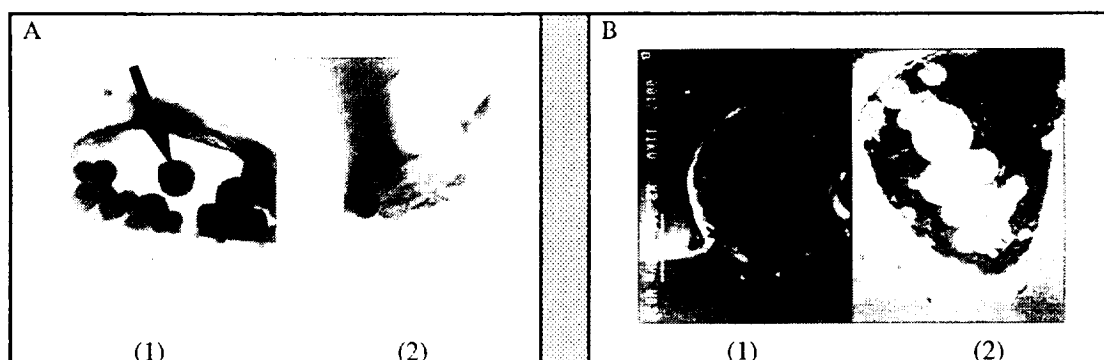

Figure 3. Micrographs exhibiting tissue preservation of *Tyrannosaurus rex* trabecular bone. A. Photomicrograph of dimorphic structures in vascular channels. Bar equals 20 μm. (1) group of structures in vessel channel resembling red blood cells. (2) Isolated red blood cell-like structure in channel. B. Scanning electron micrograph of structures in vessel channel (1). Cross section showing geometric structure in central region of structure interpreted to be the cell's nucleus (2).

Microscopic studies of this bone show excellent preservation with no secondary crystallization or infilling of sediments within the visualized blood vessel channels or marrow spaces, a condition which indicates little exposure of these tissues to infiltration by water. Electron probe analysis shows calcium and phosphorous present in amounts comparable to those seen in modern bone analyzed the same way. The amount and type of trace elements also present is likewise similar to those seen in modern bone. Transmission electron microscopy reveals a fibrous texture of the bony matrix, which may be indicative of some collagen fiber preservation, although protein specific testing must be done to verify this.

The *Tyrannosaurus rex* was a theropod, a class of dinosaur with extremely thick and dense cortical bone. It is proposed that the characteristics of these bones may have protected the internal cavities from infiltration by water borne sediments, as well as protection from UV radiation (J. R. Horner, personal communication).

PROBLEMS OF WORKING WITH "EXTINCT" BIOMOLECULES

The extreme sensitivity of the polymerase chain reaction, (PCR) which opens the door to direct analysis of DNA obtained from ancient materials, also poses the most complications. The fact that PCR technology can amplify as little as a portion of one molecule of DNA means that minute amounts of contaminating DNA from modern sources, such as bacteria, soil fungi, or human skin cells can also be amplified. Indeed, any such modern contaminant would probably be amplified preferentially over ancient target molecules, owing to the probable state of degradation of the latter. It is for this reason the

selection of primer molecules used in amplification is such a crucial step, as careful design can decrease or eliminate spurious amplification of contaminating DNA (see section on PCR in new technologies). Through studies of published sequences of extant species, it is desirable to build primer molecules from regions that would prevent the amplification of DNA from the most common sources of contamination. Also, it becomes very important to run several environmental controls at each step of the isolation and amplification process. If the gene sequences chosen for amplification flank regions of variability, or regions containing insertions or deletions, then analysis of sequence data obtained from PCR amplification of ancient targets makes contamination by modern DNA much easier to detect.

Limiting access of technicians to ancient DNA labs and equipment reduces potential sources for contamination. Frequent washing of lab surfaces with a 10% bleach solution, and continual exposure of surfaces and reagents to UV light when not in use also reduces contamination potential, as UV light is known to cross link DNA strands, thus making them unavailable for amplification through PCR. Keeping labs used in ancient DNA work separated from any labs used in modern analyses is another important requirement. Likewise, separating areas for extraction of DNA from areas designated for setting up PCR reactions also minimizes on the possibility of contamination.

But ultimately, the proof of the authenticity of any DNA presumably obtained from ancient materials comes from careful analysis of sequence data. If phylogenetic analysis of the sequences does not agree with predicted relationships based on morphological data, particularly with species such as dinosaurs which leave no modern representatives, then the DNA data must be carefully reevaluated. Also the analysis of at least two different genes or gene regions should be done, and the results of both should show similar or identical phylogenies, before any claims can be made regarding the sources of the DNA.

Ideally, DNA sequences matching obtained protein sequences would provide the ultimate proof or cross check for data obtained from ancient tissues. For example, if regions of the hemoglobin gene can be sequenced, then the amino acid sequence that specifies the primary structure of the protein can be deduced. If hemoglobin protein sequences can be obtained from the same specimen and it matches that of the inferred from DNA sequencing, then the likelihood that both are from contaminants becomes remote, particularly if the above precautions are followed for protocols.

OBSTACLES TO THE RESURRECTION OF "EXTINCT" ANIMALS

The genome of any organism, even well studied bacteria, is extremely complex. For an organism such as a human, it is estimated that a moderately sized gene is about 10,000 base pairs in length (Darnell, et al., 1990) An estimated 50,000 to 100,000 genes are required to specify a human being. With non coding regions and repetitive DNA, estimates have been made that the human genome contains billion bases. (Darnell et al., 1990) Genome size would be at least similar for most vertebrates. Some of these genes function only in the developmental stages of the organism, where timing is crucial for proper development. The organization of genes on chromosomes is also very specific, and indeed, even the number of chromosomes that carry genetic information is vital to the proper functioning of an organism. We have no way of knowing how many chromosomes may have been present in the nuclei of cells of dinosaurs, and certainly no way of knowing all of the genes involved, or their placement along the chromosomes. Without a doubt, large pieces of DNA would be forever lost. The rarity of fossil remains limits the amount of cross checking that could be done for a given DNA sequence, and for studies of this nature, a large sample size is crucial to permit any generalizations about the genome of the species to be made. The feat of mapping the human genome in its entirety has not been

achieved, even though several laboratories have been devoted entirely to this project, and we have a large supply of humans upon which to base such studies. If DNA is found to be preserved in dinosaur fossils, and if it is extractable and amplifiable, it would surely be degraded, and present in only small fragments. Trying to map the genome of an extinct organism such as a dinosaur might be an overwhelming task.

Even if enough material could be found with which, somehow, we could piece together the genome for an animal like *Tyrannosaurus rex*, other factors enter into the process of translating DNA data into a living breathing organism. It is certain that the dinosaurs were adapted to the biospheric conditions of their world, and that these conditions have changed. Their digestive systems would have had enzymes specific to the digestion of plants and other foods of that time, which may or may not be effective for foods of today. Their microbial flora, which aid in the digestion of foods, would also have been different. Their immune systems would probably have limited defenses against the microorganisms that affect life forms today. Ecosystems are incredibly delicate and interdependent. The ecosystems that supported dinosaur life are not present today, but if a dinosaur were "built" from DNA recovered from fossil bones, the DNA would not have evolved and may not have permitted the animal to function under current ecologic conditions.

So, in summary, even if it could be shown that DNA did exist in ancient tissues other than those preserved in amber, and if it could be recovered and sequenced, and if it could be pieced together from many samples to specify the genome of a dinosaur or other extinct group, far too little is known about the developmental conditions of dinosaurs and the world in which they lived to allow a "cloned" creature to survive in today's world.

BRIEF REVIEW OF CURRENT PROGRESS

In the spring of 1990, a mostly complete, largely articulated skeleton of a *Tyrannosaurus rex* was recovered from the Hell Creek formation of eastern Montana. This formation represents the youngest sediments of the Cretaceous period, and *T. rex* was among the last dinosaurs to walk the earth.

During the course of preparation of the bones of this animal it was noted that the trabecular bone contained within the long bones of the animal was not filled in with sediments or secondary crystallization, but had the look and appearance of modern, desiccated bone. Microscopic analysis showed the presence of rounded, cell-like structures localized to the vessels of this bony material (Figure 3). Electron probe analysis revealed the presence of elements such as calcium and phosphorous in the bony matrix, which were consistent with modern samples analyzed the same way. However, the rounded cell-like structures revealed a very different elemental profile than the surrounding bone. The element most predominant in these rounded structures was iron. These data led to the consideration of the possibility that perhaps the blood cells of the animal were preserved in some state, although they would have clearly been altered from the living state. This is not the first time such a possibility has been noted, for as far back as 1907, the presence of iron bearing microstructures were noted in vessel channels and the possibility that they represented blood derivatives was considered (Seitz, 1907; Swinton, 1934; Moodie, 1923).

Scanning electron microscopy of the rounded structures within the vessel channels showed them to be dimorphic, with an outer, amorphous part, and an inner part with definite pattern or structure (Figure 3). Unlike pyritic framboids, which are iron containing geological microstructures noted in the literature (Canfield and Raiswell, 1991), even under very high magnification, no crystal faces could be seen in these microstructures, and trace elements associated with the structures were consistent with those elements present in

modern erythrocytes. Given these preliminary data, it seemed further studies were warranted.

Trabecular bone was collected from the remaining long bones of the specimen while these bones were still in the plaster jacket. Gloved hands and sterile instruments were used at all times in handling the bone samples. The marrow tissues were collected immediately upon removal of remaining sediments from the bones, and before any preservative had been applied or before any handling of the bone had occurred, and the tissues were removed and stored at -20 °C under desiccation in sterile containers. Only one person had access at any time to these tissues. The possibility of contamination from human sources was controlled as much as possible.

Reverse phase HPLC revealed the presence of several apparent organic components in extracts of the bony matrix, including peaks at 265 nanometers[1] (nm), 250 nm, and 410 nm, which are suggestive of nucleic acids, possible peptides, and heme, or heme bearing compounds, respectively. These results presented the possibility that indigenous organic components were preserved within this dinosaur bone.

Preliminary attempts to extract DNA from the bone were successful. Bands which stained with ethidium bromide, and which digested to completion with DNase, were seen under UV light on agarose gels. The DNA extracted from the bone, however, was in far greater amounts and of far higher molecular weight than would be expected from any material this old. It was assumed that contamination from some source or sources had occurred at some time, but it was hoped that perhaps among the contaminating DNA, some remnants of the dinosaur DNA had been preserved as well.

The success of extraction of DNA from these tissues was repeated in a second laboratory, under more carefully controlled conditions, by at least two other experimenters. Preliminary amplifications have been done, and were also successful. The amplified products have been sequenced, and the alignment of sequences and analysis are being conducted. Further testing for reliability and repeatability will be done before such data are published.

One of the goals of our current amber studies is to extract and characterize dinosaur DNA that might be present in the abdomen of female blood-feeding midges (ceratopogonid flies) embedded in late Cretaceous Canadian ambers. The blood feeding habits of these flies are assumed based on morphological analysis of its mouth parts, which are designed to penetrate surface tissues, and on comparisons with related extant species. Prior to proceeding with the extraction of DNA from such amber-imbedded specimens, it was our aim to develop a model with which to evaluate methods for extracting and discriminating between insect and dinosaur DNA, should they be present in the abdominal cavities of the female ceratopogonid fly. The model involved the isolation of DNA from the abdominal cavity of the bee, *Proplebeia dominicana* in Tertiary ambers from the Dominican Republic in order to distinguish between bee and *Bacillus* spp. DNA. The bee-*Bacillus* association is well described (Gilliam et. al., 1990a, 1990b, Gilliam and Taber III, 1991) and these bacteria appear to be ubiquitous in the abdominal cavity of worker bees.

Based on microscopic observations of stingless bee abdominal tissue, in which bacterial cells and structures resembling endospores were seen, a study was initiated to determine whether or not *Bacillus* DNA was present in the abdominal cavity of *Proplebeia dominicana*. The primers BCF1 (CGGGAGGCAGCAGTAGGGAAT) and BCR2 (CTCCCCAGGCGGAGTGCTTAAT) were obtained from the 16s rRNA sequence of *B. circulans* (GenBank Accession number X60613) and amplify a 530 base-pair (bp) region of this gene. When tested using genomic DNA from various species of *Bacillus*, the primers amplified a 530 bp fragment in all *Bacillus* spp. tested. The primers did not

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[1] 1 nm is 1 x 10-9 meters or 1 billionth of a meter

amplify *Clostridium, Escherichia coli, Pseudomonas aeruginosa,* or *Listeria monocytogenes.*

Amber pieces were decontaminated as described by Cano et. al., (1992b, 1993) and placed in sterile glass Petri dishes and covered with liquid nitrogen until it evaporated. The cold amber pieces were cracked by the addition of a few drops of hot, sterile, physiological saline and pried open to expose the tissue. Representative samples of tissue from head, thorax, and abdomen were collected using sterile needles and stored at -70 °C until used. Samples of the processed amber were inoculated into tubes of Trypticase Soy broth (TSB) (BBL, Cockeysville, MD) to evaluate the sterility of the samples. None of the samples were positive for growth after 30 days of incubation at 30 °C.

DNA extractions from extinct species were carried out using silica powder and the chaeotropic salt guanidinium isothiocyanate (Cano and Poinar, 1993). This method has been shown to be well suited for the extraction of DNA from samples containing partially degraded DNA such as it is likely to exist in tissues from amber inclusions and has the added advantage that the DNA can be stored at -20 °C indefinitely.

The DNA extracted from head, thorax, and abdominal cavities of 9 amber-entombed bees was used as a source of templates for the PCR using BCF1 and BCR2 and bee specific primers (PDF1 and PDR3). Of the 27 individual tissue samples analyzed, only four abdominal tissue specimens were amplified by the PCR, yielding a characteristic 530 bp fragment for the BCF1 and BCR2 primers, and the 555 bp fragment from the PDF1 and PDR3 primers. All 20 environmental contamination controls (which are routinely run along with the experimental samples to monitor the degree of environmental contamination with DNA) were negative as were the amber decontamination rinses. Positive controls also yielded the expected 530 and 555 bp fragments, respectively.

Nucleic acid sequences of the abdominal tissue amplicons using BCF1 and BCR2 were very closely related to those of *B. circulans* and *B. firmus* as evidenced by BLAST and FASTA searches and CLUSTAL (Higgins et. al., 1992) sequence alignments. Phylogenetic inference analyses of the presumed fossil *Bacillus* sequences placed the nucleic acid sequences in the same sister group as *B. pumilus, B. circulans,* and *B. firmus,* all of which have been isolated from extant stingless bees (Figure 4). Ribosomal DNA sequences were clearly most similar to those of modern *Bacillus* spp. and not to *Proplebeia. Proplebeia* 18s rDNA was amplified with insect specific primers but not with *Bacillus*-pecific primers. *Proplebeia* sequences were identical to those previously published (Cano, et. al., 1992b). These sequences did not align well with 16s rDNA sequences obtained from enzymatic amplifications of bee abdominal tissue using *Bacillus*-specific ribosomal primers.These results indicated that it is possible to discriminate between *Bacillus* DNA and *Proplebeia dominicana* DNA extracted from the abdominal tissues by PCR, using taxon specific primers.

Based on the results obtained in the bee-*Bacillus* studies, a preliminary study was initiated using two Canadian amber-entombed female ceratopogonid flies. these flies possessed mouth parts with adaptations for biting large animals (e.g., moose, elephants, etc.). Enzymatic amplifications using the polymerase chain reaction was performed on DNA extraction from two separate ceratopogonid flies in Cretaceous ambers. The primers used (18sDF and 18sDR) amplify a region of the 18s rDNA gene containing a 19-base insertion in the mammalian lines,, with the expectation that a mammalian contaminant would be easily spotted. Amplification was successful using the above mentioned primers. Ostrich and alligator DNA also yielded the predicted 201 bp band whereas human DNA amplifications yielded amplicons (PCR products) measuring 220 base pairs in length. Extant DNA amplifications were performed after amplifications of extinct DNA, and in a room separate from where extinct DNA amplifications were performed. The amplified band was the correct size for a reptilian/avian sequence (201 bp). Sequences are being obtained and other primers flanking regions of phylogenetic importance are being tested.
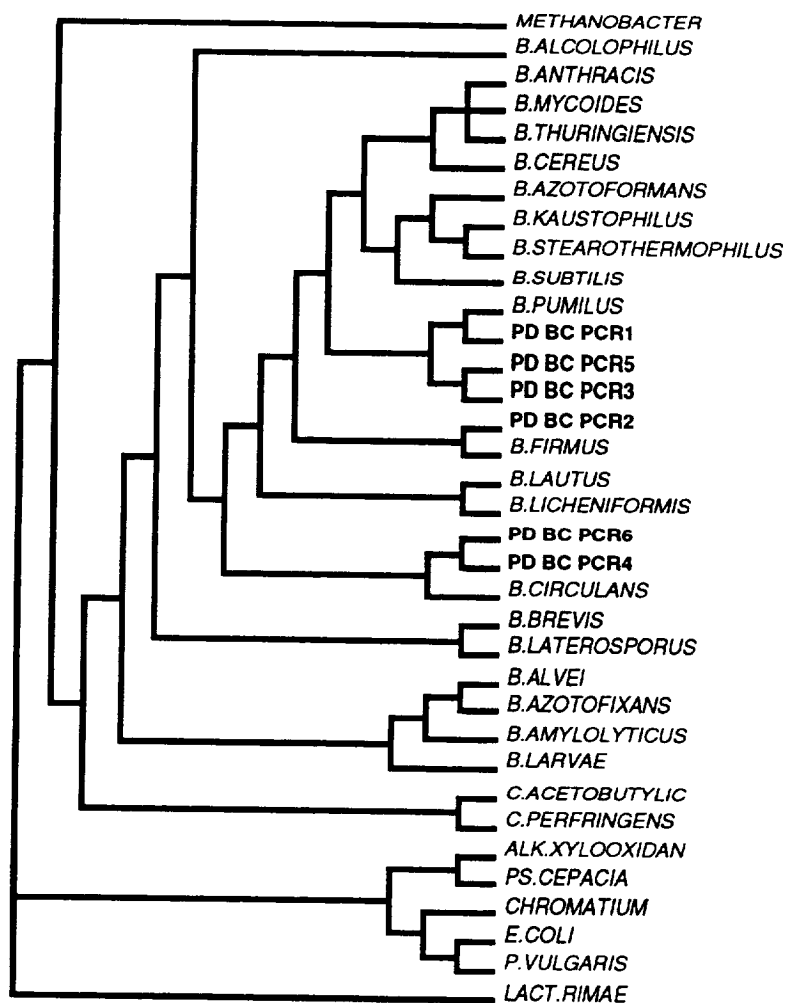
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Figure 4. Most parsimonious tree constructed from 16s rRNA sequences from amplified segments of DNA extracted from amber-entombed insects using Bacillus-specific primers. A total of six different sequences, identified as PD_BC_PCR, proceeding from enzymatic amplifications of abdominal tissue of the extinct bee *Proplebeia dominicana* in Dominican amber. Notice the phylogenetic association of the extinct DNA sequences with *Bacillus circulans, B. pumilus,* and *B. firmus.* All these three *Bacillus* spp. are common mutuals of the present-day stingless bee *Plebeia frontalis,* one of the closest living relative of *Proplebeia dominicana.*

The above described primers, however, do not amplify extant ceratopogonid flies. Primers NS1 and NS18 (which amplify a 220 bp segment of the 18s rRNA gene of these insects) were used in the successful amplification of extinct and extant ceratopogonid flies. Nucleotide sequences obtained aligned well with sequences from *Aedes albopictus* and *Drosophila melanogaster.*

The results obtained both in the bee-*Bacillus* studies and the preliminary studies with Canadian amber inclusions seem to indicate that it is possible to extract and selectively amplify DNA molecules preserved in Tertiary and Cretaceous ambers. Whether or not

dinosaur DNA can be extracted and analyzed from the gut of blood-feeding insects still remains to be verified.

IN CLOSING

As scientists, we should be fully aware of the folly of saying "impossible" or "never." So, in that light, let us imagine, in the far, distant future, walking through a forest of long extinct plants, and being surprised by a giant, lumbering dinosaur, risen from extinction, similar to the opening scenes of the movie, Jurassic Park. But the technology to achieve this scenario remains far beyond our grasp at the present time. There are far too many missing pieces of information and unsolved questions, at this time, to predict this outcome within our lifetimes.

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Dinosaur Breath:
Change, Other Kinds of Fossils and *Jurassic Park*

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Introduction

During the latest Cretaceous, before the demise of the last dinosaur, there were ferns, palm trees, and crocodiles in what is now desert in New Mexico, Seymour Island in Antarctica, and the Gobi Desert. Then things changed. Ferns, palm trees, and crocodiles no longer live in New Mexico, Antarctica, or the Gobi Desert because the climate changed. Throughout the 4.6 billion year history of the Earth, internal and external forces have caused changes in the very thin surface layer of the Earth where life exists.

Changes in the physical geography of land and water masses, atmospheric composition, or solar energy (Figure 1) reaching the Earth's surface cause the climate to change. Life changes in response to these physical changes, and life causes physical changes. For example, photosynthesis contributed much of the atmosphere's oxygen, and respiration consumes that oxygen. The reverse is true for carbon dioxide. Gases released during the weathering of rocks and from volcanic eruptions also contribute to changes in atmospheric chemistry. Gases are removed from the atmosphere when other minerals and coal are formed. Thus, life both uses and creates the atmosphere and atmospheric composition drives climate.

These perturbations of the physical equilibrium of the Earth cause an extremely complex series of responses. The feedback loops that link life to the physical environment are known as biogeochemical cycles. Large, rapid changes in the physical environment have a greater impact on the biosphere than small, gradual changes. In other words, meteorite impacts or voluminous volcanic episodes would increase the rate of extinction of living organisms because of the tremendous impact on the composition of the atmosphere and climate; the environment changes at rates too great for organisms to adapt.
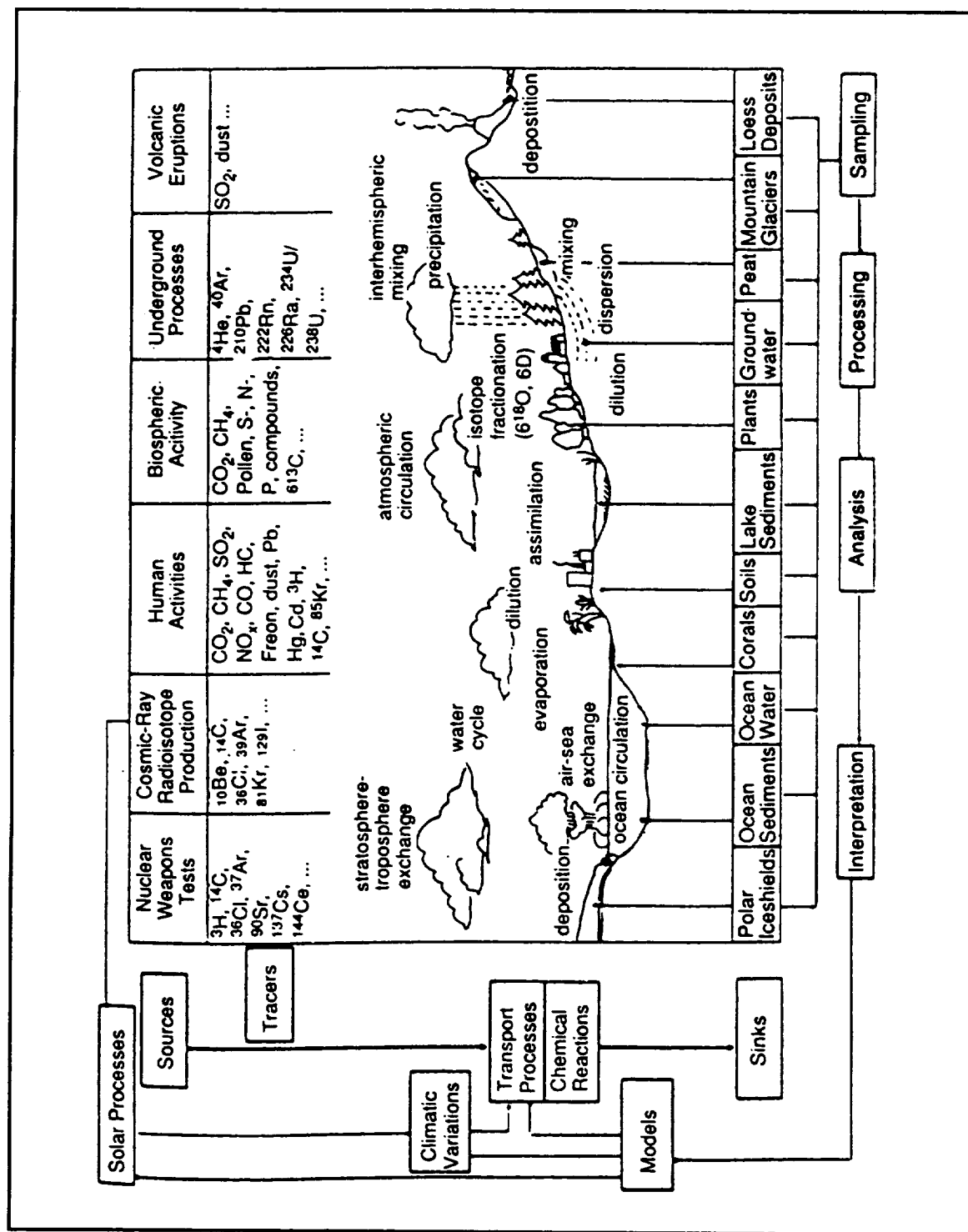
Figure 1. Geochemical tracers used to document climate changes in the geologic record, showing the natural archives in which they are sequestered and the processes through which they are deposited. (IGBP: A Study of Global Change, Report #12, 1990, p. 7.1-21).

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How are Changes in Climate or Atmospheric Composition Measured?

Change is the difference between two points--two points in space (if it is colder today in Siberia than here) or two points in time (if it is warmer here now than it was last June). Over geologic time scales, data points are collected in an assortment of natural archives depending on the time scale of interest. The record of the most dramatic recent climatic lurch--when deglaciation accelerated some 15,000 years ago--is found in ice and ocean cores, varved lake sediment cores, tree rings, and the ratios of stable isotopes. Tree rings provide information for time scales of thousands of years; ice core records extend back about 200,000 years.

Fossil pollen and charcoal provide records over approximately the past 300 million years. Records of isotope ratios of different elements are available for different time scales depending on the half life of the isotope. Ratios of oxygen isotopes analyzed from deep-sea cores have demonstrated that temperatures have varied in frequencies predicted by the Milankovitch theory (see box) (Hays, 1976). Before about 1 billion years ago, minerals provide the only information on the Earth's surfical environment.

> **MILANKOVITCH CYCLES**
>
> The Earth's orbit and rotational axis determine the latitudinal and seasonal distribution of solar radiation that is received at the top of the Earth's atmosphere. The Milankovitch or astronomical theory suggests that these changes are sufficient to explain long-term climate variability such as the glacial-interglacial cycles. Prominent periodicities of this forcing are about 100,000 yr (eccentricity of the Earth's orbit), 41,000 yr (obliquity of the ecliptic) and 23,000 yr and 19,000 yr (precession in the equinoxes) (Berger, 1977).

The study of fossils is critical to understanding the changes in the earth's environment over time. Yet abundant bones, shells, eggs, and plant and animal impressions are found over only the last 1/9th of Earth history. There are other remains of life and indicators of paleoenvironments. These are complex organic substances found in sediments whose molecular structure can unambiguously be linked with a specific precursor.

Amber: A Definition

Amber or fossil resin is a unique chemical fossil. Fossil resin is defined here in its broadest sense as any plant exudate of respectable age and is used synonymously with "amber." Others (Grimaldi, 1989) have defined amber as polymeric, terpenoid fossil resin. Most resin-producing trees are found in tropical or subtropical lowland environments suggesting that resin evolved in plants as a defense against disease-causing microorganisms and herbivores. Resin production is apparently of great value to plants because it is synthesized in many different plant families; wood impregnated with resin is

extremely durable. However, resin is not resistent to temperatures above 150°-300° C. Resins are resistant to chemical and biological degradation over geologic time.

Because the constituents of resin do not suffer the same preservation or concentration problems as other sedimentary organic molecules, fossil resins provide a unique geochemical record. This relative longevity coupled with the diversity of these complex plant products make them excellent chemical fossils.

Fossil resin or amber has been used by man throughout history as amulets and gemstones, for barter, as a waterproofing agent and protective coating, and for its medicinal properties (Fraquet, 1987). The earliest reference to amber is found in Homer's Odyssey (8th-9th century, B.C.). Pliny, in A..D. 77, correctly recognized that amber is fossilized tree sap. Because of its historic economic importance, fossil resin has been the subject of extensive chemical and physical analysis (Helm, 1891; Langenheim, 1968). Only relatively recently, however, have the analytical techniques with which to characterize mixtures of complex organic polymers been available.

The chemistry of the amber is determined by the plant that synthesized the fresh resin, the environment into which it was deposited, and the chemical, temperature, and pressure regimes to which it was exposed during diagenesis (alteration) of the sediments in which it is preserved. Resin is a complex mixture of large organic molecules, principally terpenes. Polymerization of the resin begins immediately after it is exuded by the plant. Within weeks it is in final form and is resistent to air, water, and microbial action.

The chemical analysis of resin is difficult. Infrared spectroscopy (IR), nuclear magnetic resonance (NMR), pyrolysis gas chromatography/mass spectrometry, differential thermal analysis and x-ray diffraction (XRD) have been used in attempts to analyze fresh and fossil resin and to establish relationships between them. Success has been limited though IR has proven to provide diagnostic data in some cases. There is a broad horizontal shoulder between 1230 and 1175 cm^{-1} (frequency of the electromagnetic radiation, see Figure 6), followed by a sharp peak at 1150 cm^{-1} that is diagnostic of Baltic amber (Beck, 1986). Trade routes have been determined using spectrophotometric data, and amber artifacts found in archaeological sites around the Mediterranean can be traced to Baltic sources.

Fossil resin is more common in the rock record than previously thought. It occurs throughout the world in soil, coal, and sedimentary rock. Excellent reviews of the geographic distribution of amber have been published by Barry (1932), Howes (1949), Langenheim (1964, 1968), and Fraquet (1987). Carboniferous fossil resin has been reported (Langenheim, 1964) but these "resin rodlets" from coal may be the products of pollen or cuticle rather than true resin. Most amber occurs in Late Cretaceous to Tertiary strata. Late Cretaceous resin is known from the Atlantic Coastal Palin (e.g. Grimaldi, 1989), the Western Interior of the United States (White, 1913; Bellis, 1990), Baja California (Langenheim, 1960), Israel (Nissenbaum, 1975) and France (Schluter, 1983).

Mineralogists have described and named several hundred fossil resins. Amber, however, is not a mineral and the mineralogical names are, at best not definitive. Four genetic types of fossil resin are recognized (Figure 2).

* primary resin fossilized *in situ*. The resin drops off of the tree into wet soil or, more probably, water. It is neither transported nor subjected to high temperatures or pressures.

* secondary fossil resin associated with coal; as detrital plant material is compressed and subjected to higher temperatures and pressures, the resin within the plants begins to flow and fill fractures.

* tertiary fossil resin is primary or secondary resin that has been transported. Gem quality resin such as that from the Dominican Republic or the Baltic are examples.

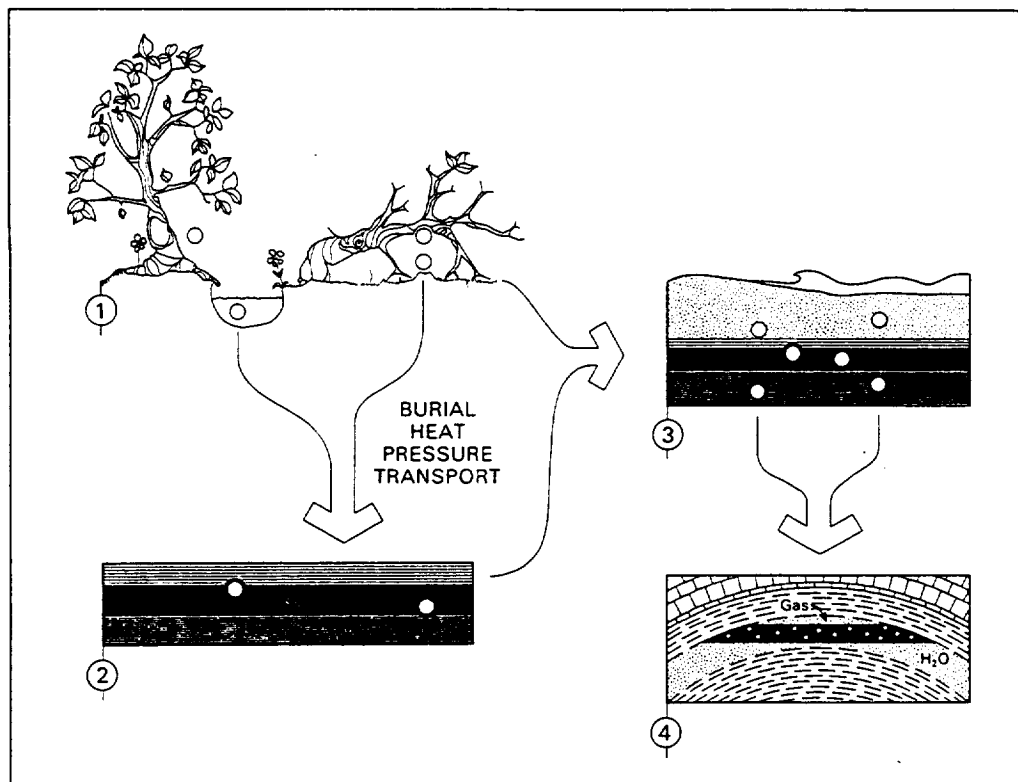* quaternary resin refers to resin products found in petroleum.

Figure 2. Genetic types of resin: 1. Primary; 2. Secondary; 3. Tertiary; 4. Quaternary (see text for descriptions) (after Bellis, 1990).

In the fossil forest, San Juan Basin, New Mexico (see Wolberg, this volume), droplets of primary resin are found associated with dinosaur bones and plant fossils. Resin is also found in petrified wood. Most amber, including that found along the Baltic and in the Dominican Republic has been redeposited. It is difficult, therefore, to determine its age. The relationship between the Fossil Forest resin and its depositional environment is easy to establish. Samples, however, are small and difficult to find, and inclusions are rare.

Physical Properties of Amber

Amber is usually "amber" colored--various shades of gold to yellow. However, green, blue, cherry red, and brown amber have been found. The significance of color is not clear although differences have been attributed to degrees of oxidation. However, that is not the whole story. Deep red and clear yellow fossil resin are known from the same locality in samples that have been exposed to identical environmental influences over long time periods. Therefore, color variation must also be due to to differences in the chemistry of the fresh and fossil resin. In some cases, fossil resin is iridescent.

The range of values for physical parameters reflects the differences in amber samples from different localities and between samples from the same locality (Table 1).

PHYSICAL PROPERTIES OF FOSSIL RESIN				
Melting point				
Baltic amber	350 - 380°C (softens at 250-300°C)		Fraquet, 1987	
Wheelerite	154°C (decomposes at 200°C)		Loew, 1875	
Density				
Baltic amber	1.08		Fraquet, 1987	
Wheelerite	1.03			
Hardness (Moh's scale)	2 - 2.5			
Crystal system	amorphous			
Ultimate analysis				
carbon	72.97 - 81.64%		hydrogen	7.91 - 10.5 %
oxygen	7.56 - 9.12%		sulfur	0.4 - 1.15%
Cleavage	none		High dielectric constant	
Fracture	concoidal		Luster	resinous or waxy

Table 1

Fossils, Chemical Fossils, and Paleowater Trapped in Amber

The chemistry of fossil resin is a source of information about the kinds of trees in the ancient environment, the presence of fossil resin in sediments provides information about the depositional and diagenetic environment, and the biological material trapped in the resin gives information about ancient plants and animals just as more typical fossils do. Most of what is known about insect evolution is known from insects trapped in amber. Resin also traps dust, air, and water. Records of atmospheric gases trapped in bubbles in ice extend over approximately the past 200,000 years. However, bubbles in resin trapping samples of air may extend as far back as 120 million years (Berner, 1988; Bellis, 1991).

The variety of animals and plant tissues, organs, and whole animals trapped in amber is well known. Flowers, pollen, wood, leaves, insects, geckos, and hair have been identified. Microbes in amber are less well known.

The soft tissue in some plant and animal specimens in amber is well-preserved and may provide a rich source of material for molecular phylogenetic (evolutionary) studies. Yes, the extraction of nucleic acids from fossil resin as in *Jurassic Park* is possible. And cloning a dinosaur from DNA trapped in amber would be spectacular. Before that happens, however, techniques for extracting small fragments of nucleic acids or proteins from fossil resin must be developed. Amber melts at relatively low temperatures so the mere fact that it has survived indicates that temperatures throughout its depositional history have been moderate, increasing the possibility that fragments of nucleic acids or proteins have survived. Fragments of nucleic acid could be replicated and sequenced to use for phylogenetic studies (see also, Higby-Schweitzer and Cano, this volume).

Amber with hydrous inclusions is valuable to the gem collector and to the paleoecologist. The ratios of stable isotopes of hydrogen and oxygen in rain water is related to climate. Thus, ancient water trapped in amber may be used to describe ancient climate. The fact that amber traps water is also evidence that some amber samples don't leak and, hence, their chemical contents are not contaminated.

Gaseous inclusions in amber occur in a wide variety of shapes, sizes, and abundances. Some inclusions in large, clear, specimens are visible to the naked eye. Large bubbles are often parallel to banding suggesting that they have been trapped in successive flows of resin (Figure 3). Resin flows out of the tree, hardens, then flows again trapping air. The density of small inclusions affects the color and density of fossil resin. "Ivory" or "milky" amber is opaque because there are many microscopic bubbles. Other inclusions are attached to plant or animal detritus suggesting that the gases are the products of decay of the biological material (Figure 4).

Analysis of Bubbles in Fossil Resin

Samples of fossil resin with bubbles are crushed within a vacuum chamber and the released gases are analyzed by mass spectrometry (Figure 5). The interpretation of the analyses of the gaseous contents has been controversial. Some have concluded that the mixture of gases included in amber represents the paleoatmosphere at the time the resin was extruded (Berner, 1988; Bellis, 1991). Others have argued that amber is leaky, that the gases are modern air dissolved in the fossil resin. A third possibility is that the resin outgases as it is polymerized and fossilized. Gases may also be given off by the decaying plant and animal material trapped in the resin or in the surrounding sediments.

From our studies, we have concluded that the bubbles are mixtures of all of the above and that the ratio of oxygen to nitrogen in them is stable over time. We interpret the analyses of gases from Lake Cretaceous resin as indicating that the atmosphere at that time
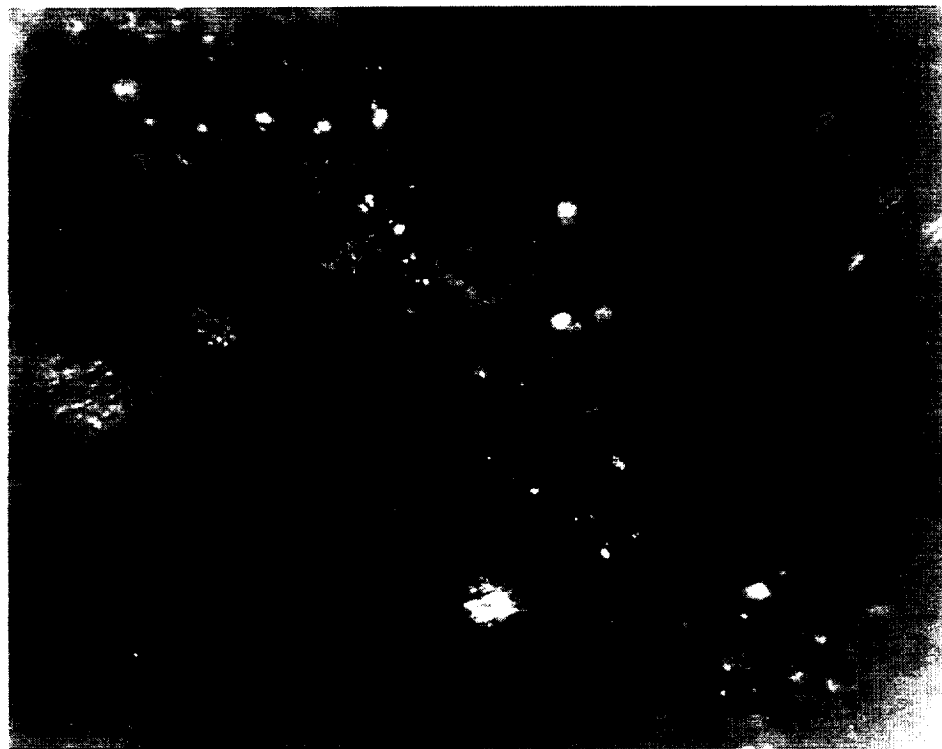
Figure 3. Gaseous inclusions in amber from New Mexico. At least some of these inclusions preserve samples of Late Cretaceous (72-74 million year old) atmosphere. Note the parallel banding indicating that successive flows of resin occurred.

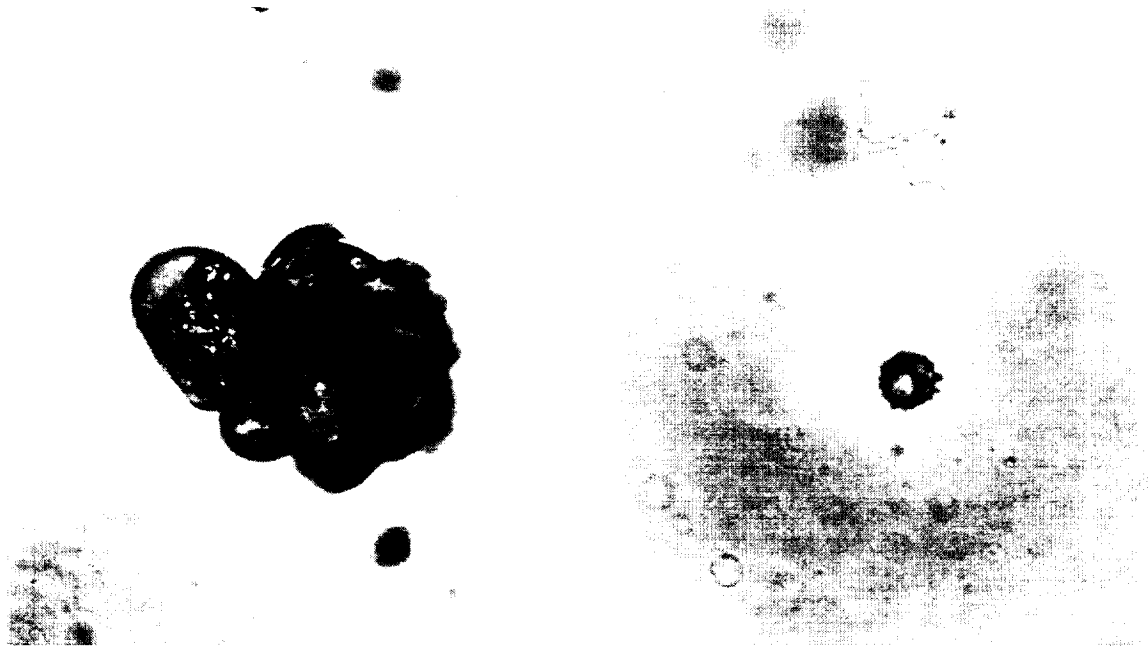Figure 4. (Left) Clumped single cells in Late Cretaceous (72-74 million years old) amber from New Mexico. Note the preservation of the cell walls and cellular contents. (Right) A dark spore or pollen grain in center of picture. Note translucent larger pollen grain at top.
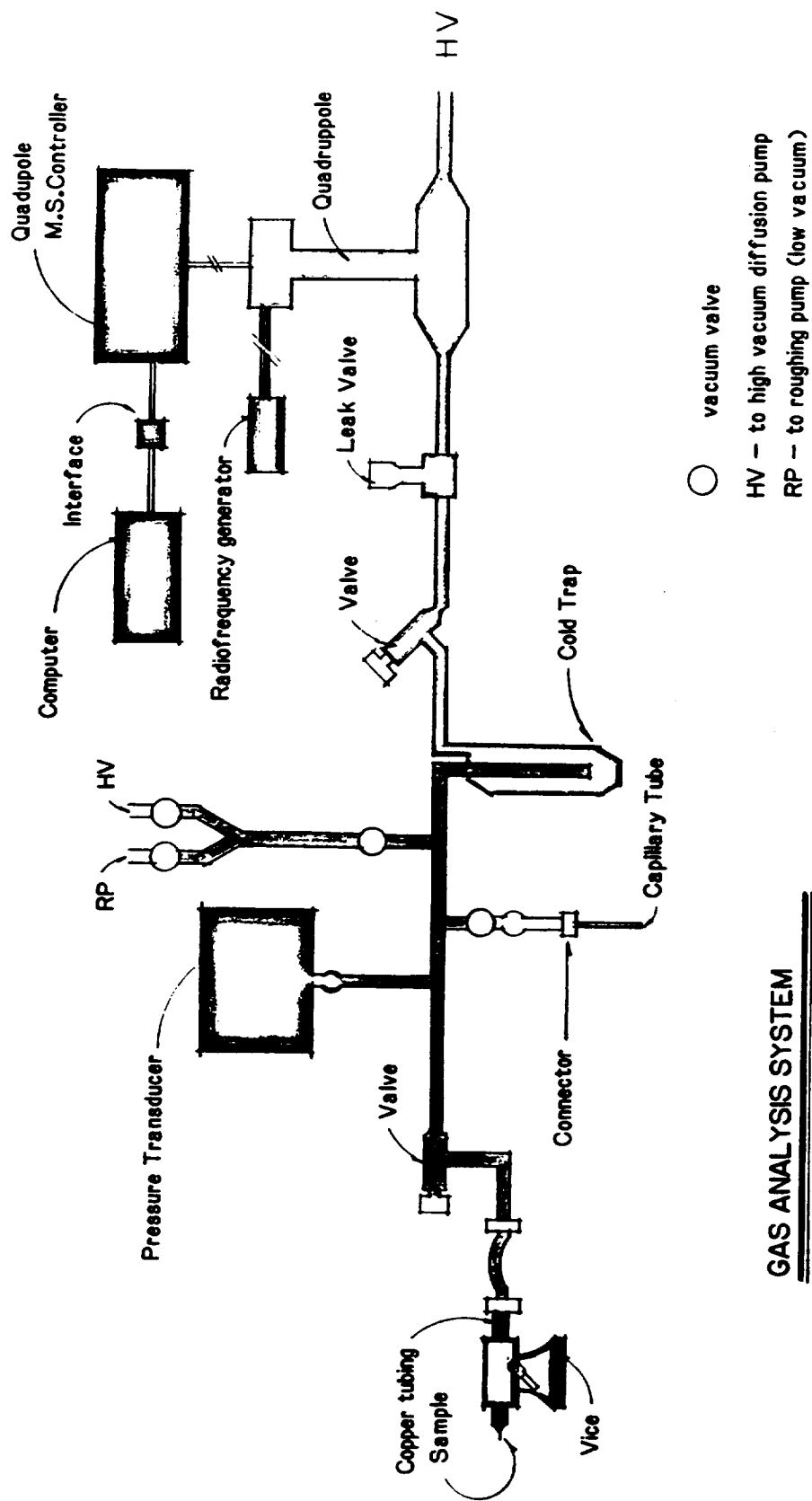
GAS ANALYSIS SYSTEM

Figure 5. Gas analysis system for studying inclusions in amber. Process begins at left where the amber is crushed in a copper tube.

1 Baltic succinite: deep clear yellow bead.

2 Baltic succinite: dull, cloudy yellow bead.

3 Baltic succinite: clear, sherry coloured with large-scale crazing.

4 Oriental: Burmite clear, mid-sherry amber. Carved figure.

5 Oriental: dark clear, polished modern cabochon 'from China'.

6 Oriental: light, clear, polished modern cabochon 'from China'.

7 Sicilian: polished sherry-coloured amber.

8 Sicilian: sherry-coloured clear, rough.

9 Sicilian: dark red, rough.

10 Romanian: Buzau Province; dark, clear yellow, typically cracked internally.

11 Romanian: Buzau Province; light clear yellow, cracked internally.

12 Dominican: green-yellow.

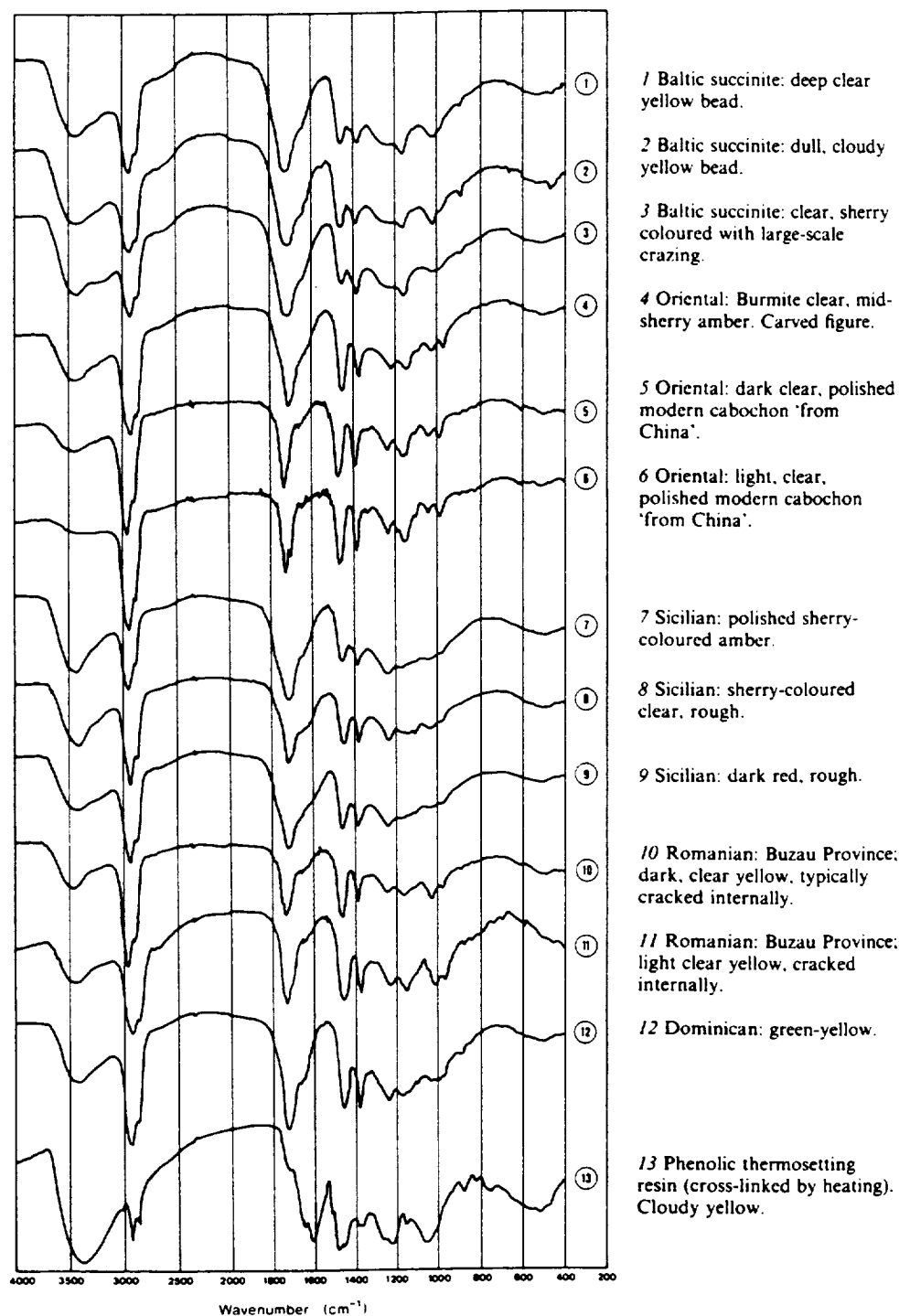*13* Phenolic thermosetting resin (cross-linked by heating). Cloudy yellow.

Wavenumber (cm⁻¹)

Figure 6. Infrared (IR) absorption spectra of different synthetic (13) and fossil resins (1-12). Units are percent transmission (y-axis) at wavelengths (x-axis) ranging from 4000 cm⁻¹ (waves per centimeter) to 400 cm⁻¹. Note the shoulder between 1250 and 1175 cm⁻¹ followed by a peak (pointing down) at 1150 cm⁻¹. The peak suggests absorption by a carbon-oxygen bond and is characteristic of Baltic amber and many North American Cretaceous amber samples from the Atlantic Coastal Plain. (From Fraquet, 1987.)

was at least 25% oxygen (today's atmosphere is about 20 % oxygen). It is thought that atmospheric carbon dioxide was six times what it is today (Berner, 1989)--a true "greenhouse." Mineralogical evidence and computer models support the interpretation that the Cretaceous atmosphere was quite different from the modern atmosphere. There is substantial evidence that the Earth's atmosphere has not evolved linearly over time. It is not clear, however, if climate change is the cause or result of changes in atmospheric composition. The search for evidence of past climates and for samples of pristine paleoatmospheres has become more important in the past 15 years as we recognize modern changes in atmospheric compostion. The ozone hole and the greenhouse effect and their impact on climate, continue to attract attention. Chemical-, macro-, and microfossils provide the only available record of past atmospheres and climates and the context in which to evaluate the impact of humans on the Earth's biogeochemical systems.

General circulation models (GCMs) integrate data points to predict the response of biogeochemical cycles to changes in the Earth's physical envelope. While our understanding of biogeochemical cycles has increased dramatically, it is clear that the uncertainty associated with predictions of future climate scenarios is high. (Even two-day weather forecasts are not very certain.) GCMs are now being used to describe past climates. Unlike predictions for the future, this output can, indeed, be verified in the rock record.

Dinosaurs walked around breathing various atmospheres and survived climatic fluctuations for about 140 million years; modern people have been here less than 50,000. Let's tread lightly.

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Digital Image Metamorphosis as a Research Tool for Paleontology

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INTRODUCTION

This is an exciting era to be a scientist, due to the increasing levels of technology available to us; particularly due to the advances that have been made in the field of computer science. Advances in electronic technology have made computer hardware very powerful and affordable, while advances in software design and human/computer interfaces have made computers more natural to use. Computers have been utilized in nearly every field of scientific study, permitting new levels of development in those fields that wouldn't be possible otherwise. Computer graphics are useful visualization tools that help scientists understand complex data, and convey ideas to others.

Digital image metamorphosis, or morphing as it is commonly called, is one such visualization technique, and we will examine how paleontologists can utilize morphing to do research that would be very difficult, if not impossible to do without it. Morphing creates a smooth transition from one image to another, by generating any desired number of intermediate images between two source images. Several mathematical calculations have to be performed for each pixel in the intermediate image being generated. A typical image of 512 by 512 pixels, would require several million calculations to generate the whole image. This would be very tedious and time consuming for a human to do, but is easily accomplished by a computer.

MORPHING AS A RESEARCH TOOL IN PALEONTOLOGY

One reason we are morphing dinosaurs at the Museum of the Rockies is to help us visualize how dinosaurs grow. A hatchling dinosaur is very small and undergoes dramatic changes as it grows through the stages of nestling, juvenile, sub-adult, and adult. We don't have a complete growth series for most species of dinosaurs, so it is very useful to create the intermediate images between the specimens that we do have. When the generated images are animated, they can reveal patterns of development that may not be apparent otherwise.

Animation of limbs, joints, and musculature is another use for morphing planned for the future here at MOR. As an example, we could morph an image of a limb in an extended position with one in a bent position, and the computer would generate the intermediate positions, allowing us to more easily study joint movement.

Morphing could also be used to check the linearity or degree of non-linearity of evolution. If we morphed specimens for which there is a very large fossil record, such as marine fossils, would the morph of a 100 million year old fossil with a 200 million year old fossil accurately represent a 150 million year old fossil? If not, we could find the age for that species where there was a close match, and determine the degree of non-linearity for that case. In a study such as this it would be necessary to create morphs between specimens much closer together in age, perhaps every 10 million years apart, and ranging over several hundred million years. It would be interesting to see what types of patterns would develop on an evolutionary timescale. It would also be interesting to morph species of dinosaurs with their ancestors to see animations of how they changed over several million years. As an example, consider following the changes in posture, limb development and size between a Jurassic *Allosaurus* and Cretaceous *T.rex*.

In one study, we morphed the skull of a nestling *Maiasaura* with that of an adult *Maiasaura*(figure 1). We found that the morph image half way between the nestling and the adult differed in several aspects from the actual specimen corresponding to that developmental stage. The reason for this is that the morphing program creates a linear interpolation, and we know that dinosaurs don't grow linearly. They grow more rapidly when they are younger, and some bones grow faster than others.
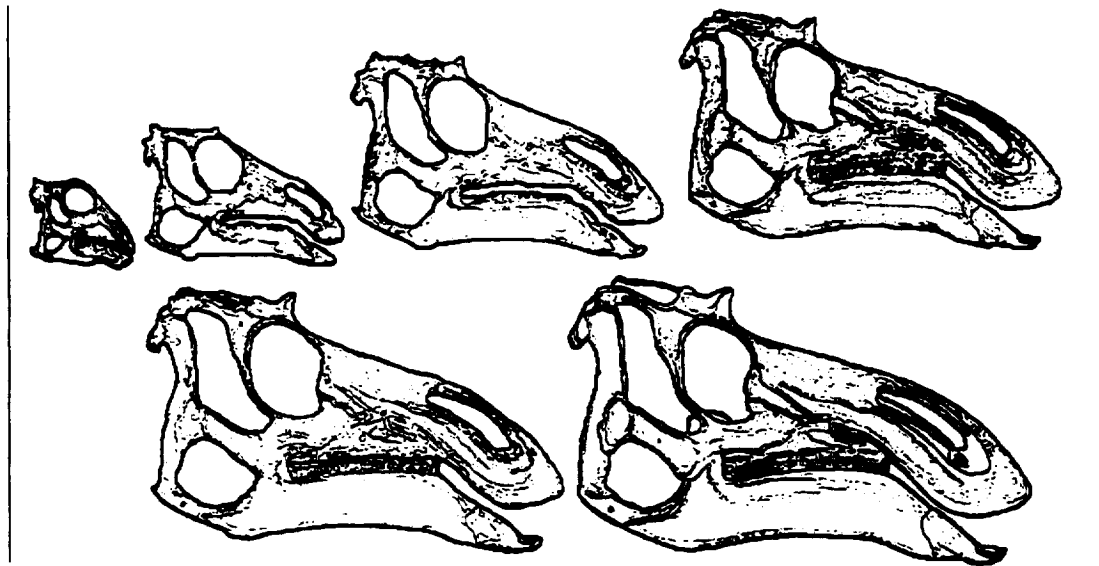

Figure 1 - A *Maiasaura* growth series. The top left and bottom right are source images, and the rest are computer generated images.

Using a species for which we have a more complete growth series, such as the *Hypacrosaurus*(figure 2), we will determine mathematical functions that approximate the growth rates for individual bones for that species, modify the morphing program, and apply those functions when we create morphs of other species. This may enable us to more accurately represent the growth series for some species that have few collected specimens.
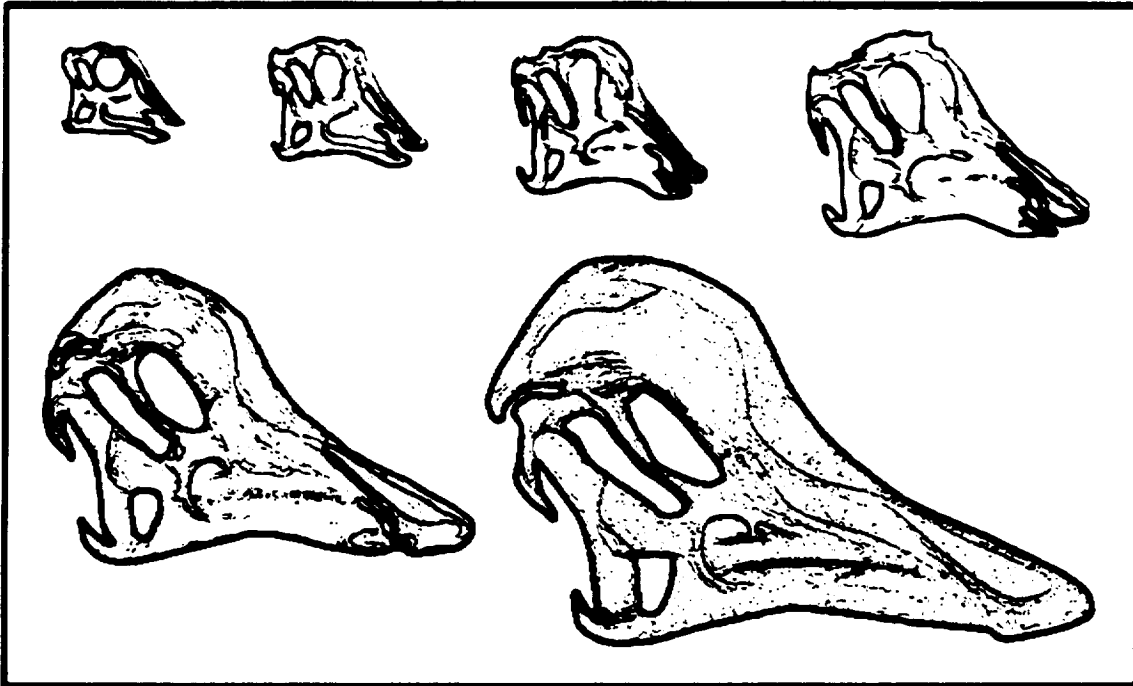
Figure 2 - A *Hypacrosaurus* growth series. The top left and bottom right are source images, and the rest are computer generated images.

MORPHING SOFTWARE AND TECHNIQUES

The morphing software that we use was written as part of my master's thesis for computer science. It was developed on a Silicon Graphics Indigo Elan, written in the language C and uses the X-11 windowing system. The software is fairly simple to use (it's always easier for the programmer who wrote it) and the computer does most of the work.

The first step in creating a morph is to acquire the beginning and ending source images. This may entail scanning in photographs, drawings or some other form of artwork, or capturing images that are already in digital form, such as CT or MRI images. The source images must be the same size, which may necessitate cropping and scaling.

The next step is to add control lines to corresponding features in the beginning and ending source images(figure 3). The computer uses the control lines as weighted boundaries for determining which pixels to sample in the source images so it can calculate the color for each pixel in the morph image. Control lines are required on the features in each source image that are important for the morph image. Usually this includes eyes, ears, teeth, bones, and the outline of the bodies, but depends on the characteristics of the images being morphed. The pixels that are close to control lines in the source images morph closely to the control lines in the morph image, and the pixels that are farther away from control lines get blended smoothly, which means the

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background in the morph image is usually smeared. The computer
uses the control lines on the source images to create similar
control lines for the morph image. It does this by averaging the
endpoints of corresponding control lines in both of the source
images and drawing lines between the averaged endpoints on the
morph image. A slider bar on the morph image window controls the
percentage of averaging done, enabling incremental morphs between
the two source images.

For an animated morph sequence we usually generate 25
intermediate images which gives us a smooth animation since there
is very little change between successive images(figure 4). In
the *Hypacrosaurus* growth series, we used three source images,
with 25 intermediate images between each. Since the current
morphing software creates linearly interpolated images, to create
a more accurate growth series, it would be necessary to morph
between several source images, as we are going to do in a new
study with the *Hypacrosaurus*. In this study, we are going to use
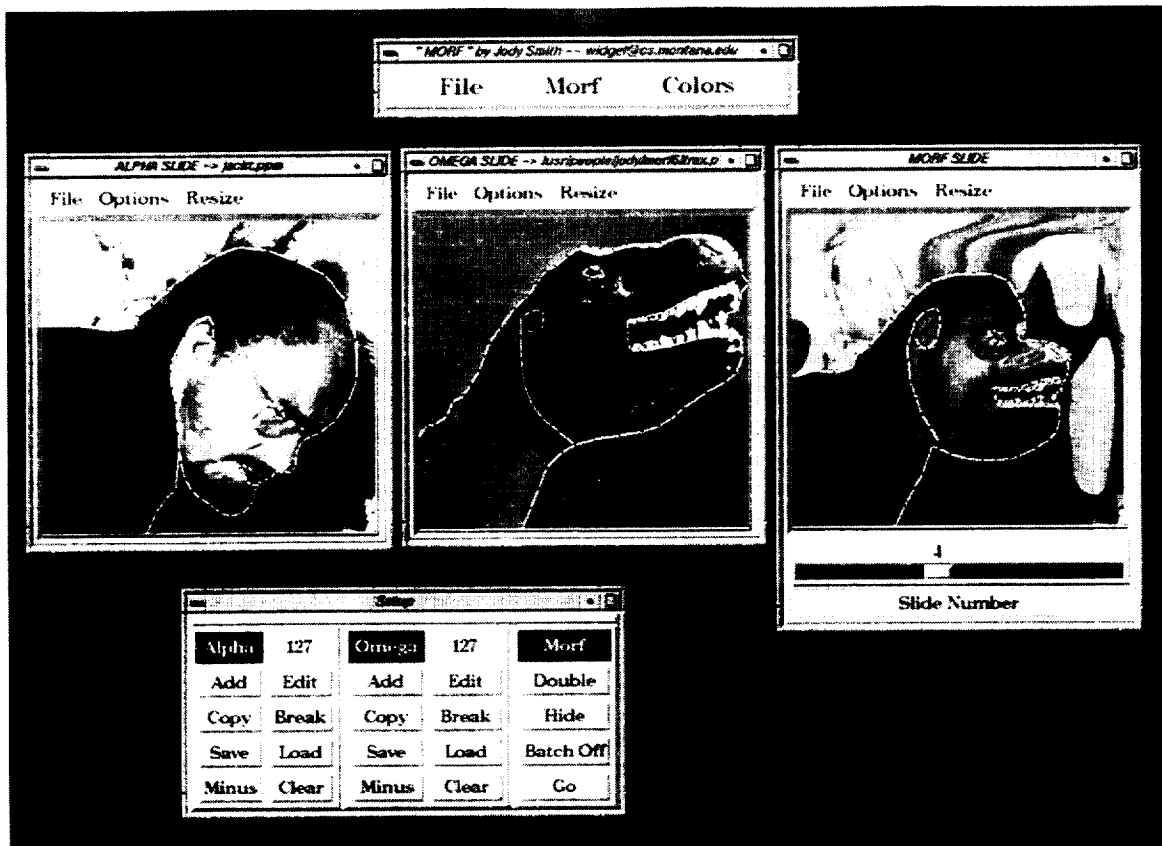images of a hatchling, nestling, juvenile, sub-adult, and adult
Hypacrosaurus.

Figure 3 - A morph between paleontologist Jack Horner and a
T.rex, showing the control lines on the source images and the
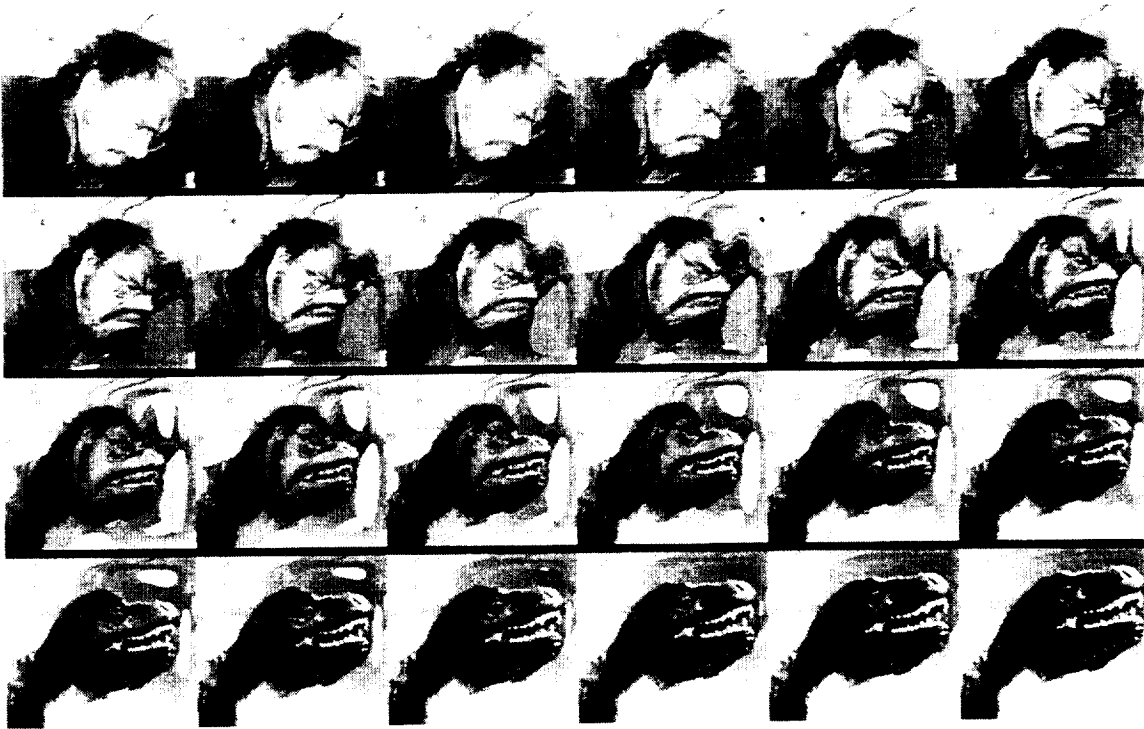smeared background on the morph image.

Figure 4 - A morph series created for animation. The first and last images are source images and the rest are computer generated. Note how little change occurs between successive images.

CONCLUSION

Computer use in paleontology is still in it's infancy. The above represents only the beginning of the list for applications of computer imaging and morphing technology to the field of paleontology. As careers become more specialized, and scientists become more computer literate, more applications will come to light. The potential for computers as a tool in paleontological research seems limited only by one's imagination.

Vegetation of the Dinosaur World

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INTRODUCTION

The process of photosynthesis is critical to the existence of almost all the Earth's ecosystems by providing the fundamental mechanism through which the Sun's energy is harnessed to convert carbon dioxide and water into sugars and oxygen. These sugars ultimately provide the basic source of energy (primary production) on which most life depends. In terrestrial ecosystems macroscopic land plants are responsible for virtually all primary production and therefore provide the basic sustenance that supports all land animals, either directly or indirectly. An accurate knowledge of Mesozoic plants and vegetation is therefore critical to understanding the ecology of dinosaurs and the ecosystems in which they flourished. Similarly, because large herbivorous dinosaurs must have exerted a major influence on terrestrial ecosystems some knowledge of dinosaur biology is crucial to understanding the ecological pressures to which Mesozoic plants were subjected. Because there is also a close correlation between the climate of an area and the kind of vegetation that it supports, fossil plants also provide important evidence on the paleoclimates of the dinosaur world.

In this paper we briefly consider the nature of the evidence from which the kinds of plants and vegetation that coexisted with the dinosaurs can be inferred. We then briefly review current knowledge of Mesozoic vegetation and the plant fossil record, and provide an outline of Triassic, Jurassic, and Cretaceous vegetation. In particular we highlight the major change in the Earth's vegetation that occurred during the mid-Cretaceous (c. 110 myr BP) with the transition from a flora dominated by ferns, conifers, and cycad-like plants to a flora more like that of the present, which is dominated by flowering plants (angiosperms). Finally, we speculate briefly on some of the major kinds of interactions through which the biology of plants and the biology of dinosaurs may have become intertwined.

THE NATURE OF THE PLANT FOSSIL RECORD

The fossil record of land plants, like that of all other terrestrial organisms, is heavily biased toward those species that live in or near suitable environments in which their remains can be preserved. In general such environments occur in areas where sand or mud is being deposited (river valleys, coastal lowlands) rather than areas in which erosion

is dominant (hillsides). Our concepts of Mesozoic vegetation, as for our concepts of dinosaur communities, are therefore substantially constrained by processes of selective preservation that incorporate a strong ecological bias. A further difficulty with the plant fossil record is that it consists predominantly of plant parts (e.g., leaves, pollen grains) rather than whole organisms. One practical consequence of this natural process of disarticulation is that paleobotanists assign names to individual organs rather than to whole plants, but a more serious consequence is that a great deal of effort must be expended in trying to determine which plant parts may have been produced by the same species. For example, in one common cycad from the Jurassic the leaves are referred to as *Nilssonia*, the seed-bearing (female) cones are referred to as *Beania,* and the pollen producing (male) cones are known as *Androstrobus*. In this case we know quite a lot about a single fossil species yet we are still missing important information such as the size of the plant, the branching patterns of its stems, the kind of wood that supported it, and ecological data on the environments in which it occurred. Unfortunately, the majority of Mesozoic plants are known from only dispersed pollen grains or spores and therefore our ability to reconstruct Mesozoic vegetation is severely constrained.

MAJOR COMPONENTS OF MESOZOIC VEGETATION

Notwithstanding the difficulties of incomplete ecological and morphological preservation, more than a century of paleobotanical research has now provided a good overall picture of the kinds of plants that were important in Mesozoic vegetation. Two main groups are represented: seed plants, and "pteridophytes", a heterogeneous group of land plants that lack seeds and that are dispersed by spores. Among seed plants there are several Mesozoic groups that are now totally extinct (e.g., Bennettitales, Czekanowskiales), while others (e.g., cycads, conifers and *Ginkgo*) still have living representatives. In addition, angiosperms, which first appear during the Early Cretaceous, now dominate the vegetation of most parts of the world. Figures 1-3, 5 and 6 illustrate representatives of these major plant groups.

"Pteridophytes"

"Pteridophytes" are a heterogeneous assemblage of herbaceous plants that include the ferns, clubmosses (lycopods), and scouring rushes (horsetails). The origin of all of these groups occurred during the Paleozoic but they were still undergoing important modernization through the Mesozoic. Together these groups comprised the dominant herbaceous component of Mesozoic vegetation, particularly in wet places. Some "pteridophytes" would also have been important in the forest understory and as ground cover, as well as in more open, drier habitats such as those occupied today by grasses.

The clubmosses (lycopods in the broad sense) are one of the most ancient groups of land plants and all three of the major lineages that are present today (Lycopodiaceae, Selaginellaceae, Isoetaceae) were also present during the Mesozoic. The giant clubmosses of the Late Paleozoic had disappeared before the Triassic but herbaceous fossil plants resembling the modern genus *Lycopodium* were undoubtedly present during the Mesozoic, as were fossil plants resembling the modern genus *Selaginella*. To judge from the abundance of their megaspores and megafossils in Mesozoic rocks, fossil plants resembling *Isoetes* were also common, particularly in areas that were either permanently wet or at least occasionally inundated by water. None of these groups of lycopods appears to have been a major component of Mesozoic vegetation.
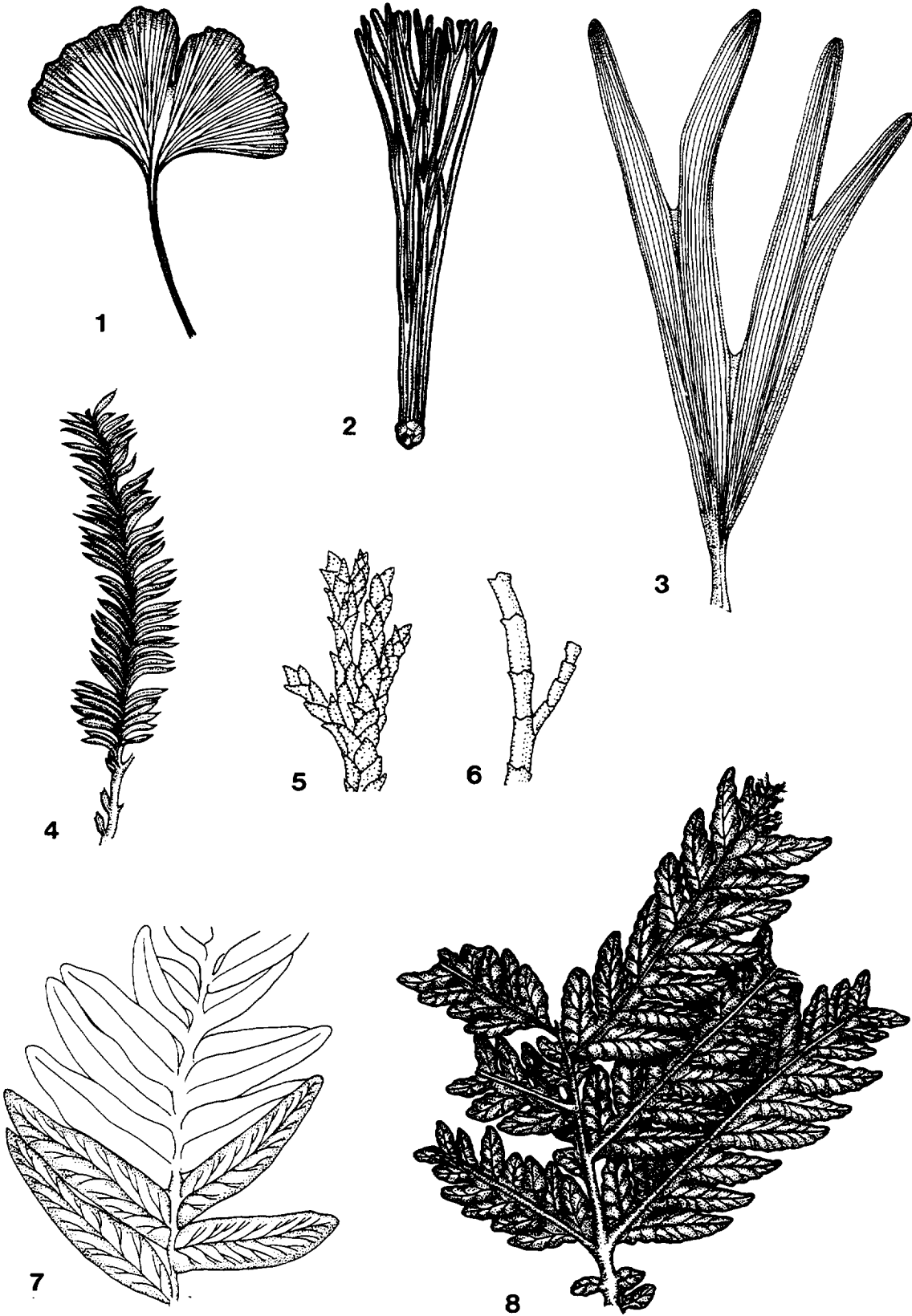
Figure 1--Representative Mesozoic plants. 1-3, leaves of Ginkgoales and Czekanowskiales. 1, Ginkgo, x 1.5. 2, Czekanowskia, x 0.4. 3, Sphenobaiera, x 0.8. 4-6, conifer foliage. 4, Stachyotaxis, x 1.5. 5, Hirmeriella, x 3. 6, Frenelopsis, x 3. 7-8, seed fern foliage. 7, Pachypteris, x 0.8. 8, Lepidopteris, x 0.8.
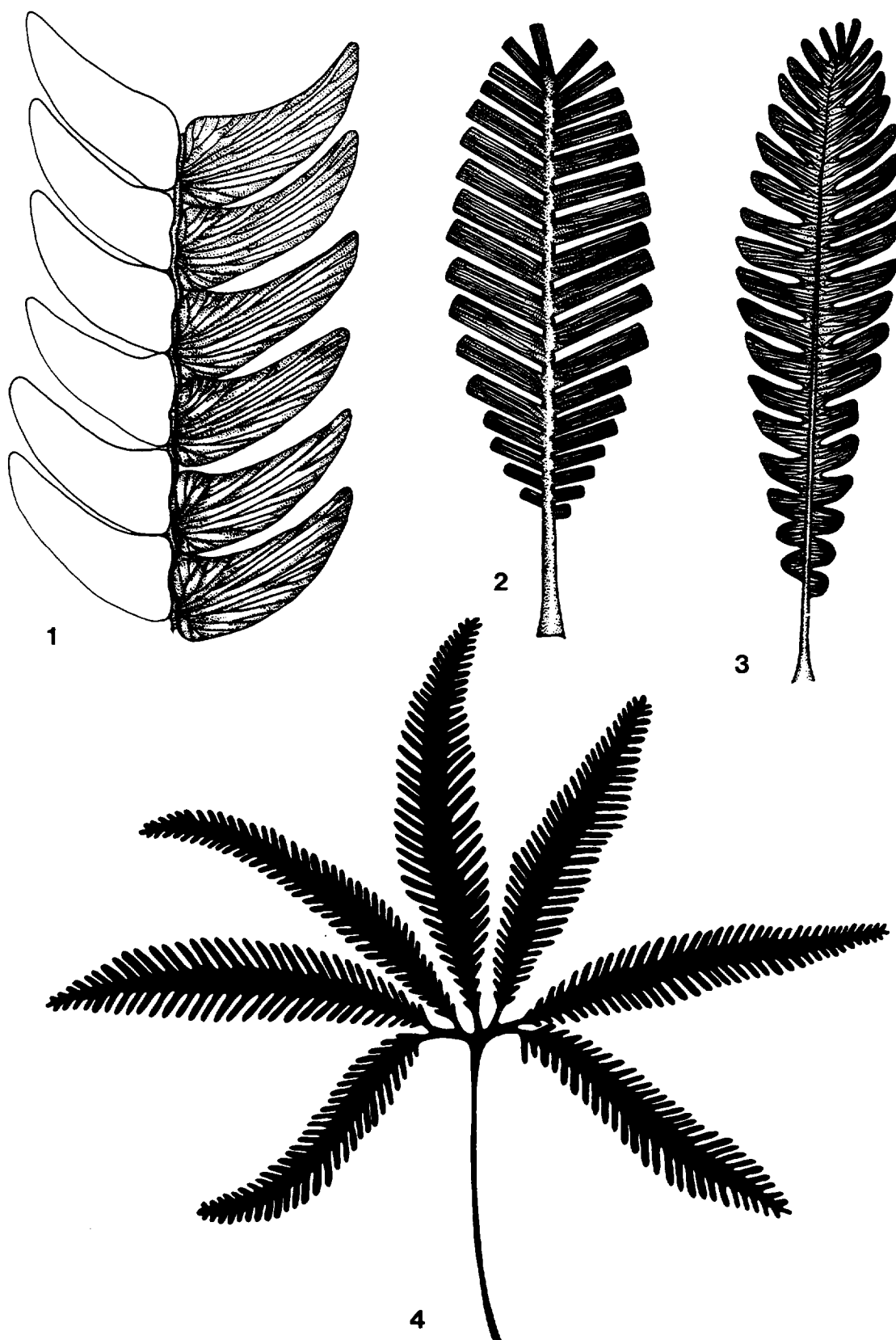
Figure 2--Representative Mesozoic plants. 1-3, Bennettitales foliage. 1, Otozamites, x 1.5. 2, Zamites, x 0.5. 3, Pterophyllum, x 0.5. 4, foliage of the fern Phlebopteris, x 1.5.
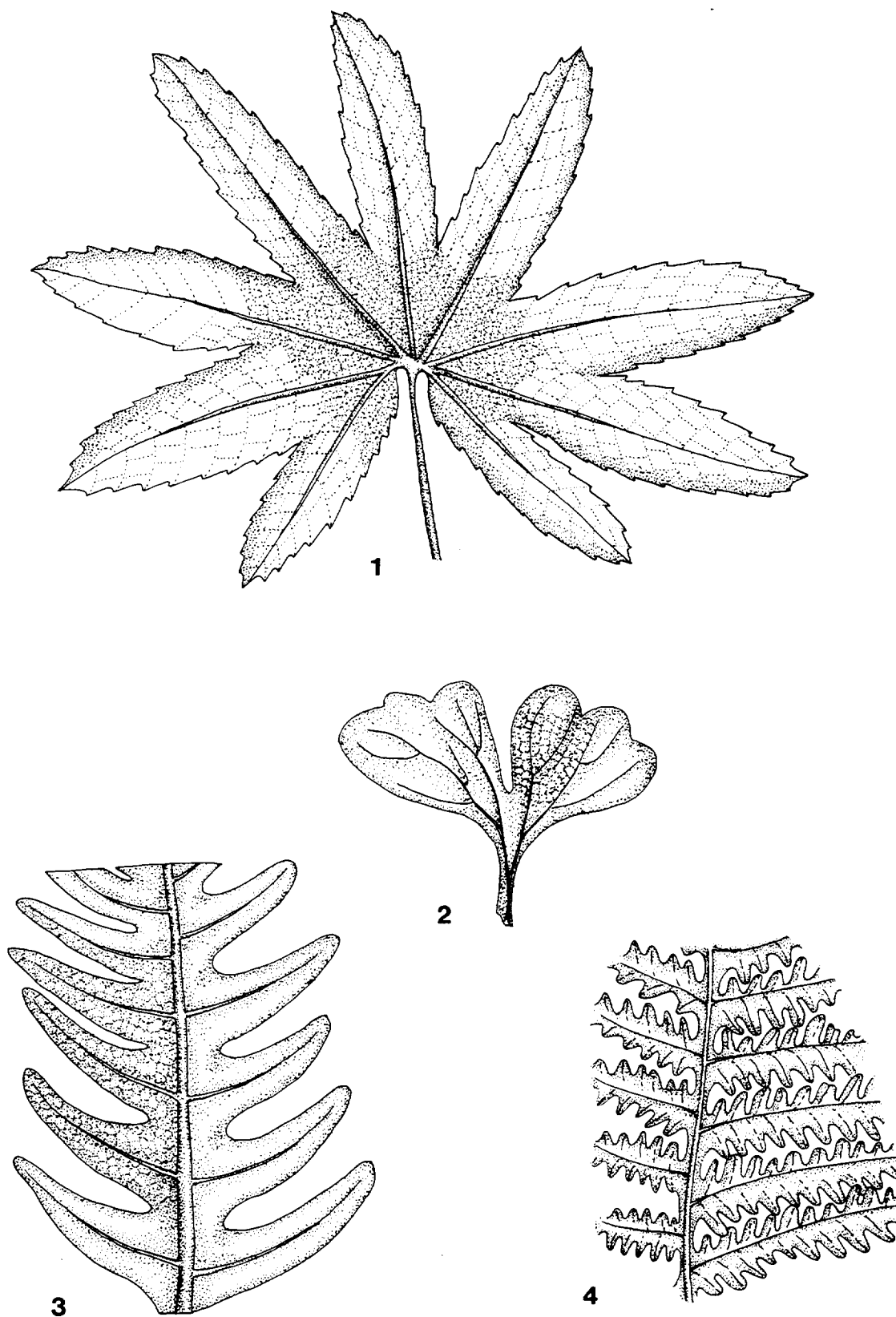
Figure 3--Representative Mesozoic plants. 1-4, fern foliage. 1, <u>Clathropteris</u>, x 1.5. 2, <u>Hausmannia</u>, x 1.5. 3, <u>Dictyophyllum</u>, x 1.5. 4, <u>Piazopteris</u>, x 1.5.

Equisetum-like plants, which are first recognized in the fossil record about 350 myr BP, are a minor but frequent component of Mesozoic fossil floras. Again they seem to have been particularly abundant in damp habitats, and in ecology as well as form they appear to have been very similar to their living relatives.

Ferns were both more diverse and more abundant in Mesozoic vegetation than clubmosses and *Equisetum*-like plants. The Mesozoic was a very important time in fern evolution because while the origins of the group extend back into the Mississippian (c. 323 myr BP) it is not until the Triassic that we see the first appearance of many families of ferns that are still represented today (e.g., Dipteridaceae, Gleicheniaceae, Matoniaceae, Schizaeaceae). During the Late Cretaceous and Early Tertiary, in association with the diversification of angiosperms, there is evidence for the first appearance of many other fern groups, especially those that are typically associated with damp shaded habitats, such as tropical rain forests.

"Cycadophytes"

One of the most striking characteristics of Mesozoic fossil floras is the presence of abundant cycad-like leaves. Frequently "cycadophyte" leaves dominate fossil assemblages from the Triassic (e.g., Basle, Switzerland) and Jurassic (e.g., Yorkshire, U.K.) and on average they account for 20-30% of the species recorded from most Mesozoic floras. In some Mesozoic floras cycad-like trunks may also be common. The Mesozoic is often referred to as the age of cycads, but it was recognized early in this century that two different groups were represented among the "cycadophytes": true cycads (Cycadales) and the extinct Bennettitales (or Cycadeoidales). Thus "cycadophytes" include two lineages of important Mesozoic plants that are probably not closely related. True cycads, which have a fossil record that extends back to the Permian (c. 245 myr BP), achieved their greatest diversity during the Mesozoic but are represented today by eleven living genera and about 120 species. There are also indications that some of the extinct forms may have been significantly different from their modern relatives in important aspects of their growth habit and biology. Bennettitales first appeared during the Late Triassic and became extinct sometime during the Late Cretaceous. Despite their initial confusion with the cycads, the Bennettitales differ significantly from them in many aspects of their structure including the flower-like aggregations of their reproductive organs, the manner in which the seeds are borne, and details of the leaves (stomatal structure).

Conifers

Conifers first appear in the fossil record during the Late Pennsylvanian and first rise to prominence in terrestrial vegetation during the Permian. However, Permian conifers differ in several important respects from their living relatives and it is not until the Mesozoic that conifers begin to more closely resemble their living relatives. The Mesozoic is thus an important period of modernization in conifer evolution, and it is during this interval that we see the first evidence of all seven extant conifer families. Throughout the Mesozoic conifers are a major component of the vegetation, and often comprise about 20% of the species recorded in fossil floras. They were particularly important at higher latitudes and the group continues to dominate the vegetation of some areas in the Northern Hemisphere up to the present day.

Other Gymnospermous Seed Plants

In addition to cycads, Bennettitales, and conifers, a variety of other "gymnosperm" groups are also represented in Mesozoic floras, and although they rarely dominate fossil assemblages, in some areas they were undoubtedly important elements in Mesozoic vegetation. A few of these groups still have living representatives (e.g., Gnetales, *Ginkgo*) while others (e.g., Caytoniales, Czekanowskiales) are now extinct. Such extinct gymnosperms are especially problematic for understanding Mesozoic vegetation because they have no clear modern analogs to guide interpretations of their ecology. Thus in terms of structure, biology, and ecological attributes these are some of the Mesozoic plants about which we know the least. It has been suggested that the ancestors of the angiosperms lie among these extinct groups.

Angiosperms

Among living plants, angiosperms (flowering plants) are more diverse than all other groups of land plants put together (c. 250,00 - 300,000 species), and they dominate the vegetation of all modern terrestrial ecosystems with the exception of boreal conifer forest and moss-lichen tundra. As far as we can currently determine, angiosperms were totally absent from the Earth's vegetation for most of the Mesozoic. Fossil angiosperm pollen grains and leaves are first recorded at low levels of diversity and abundance in the Early Cretaceous (Valanginian c. 140 myr BP) and over the next 30 million years they increase dramatically in both diversity and abundance to become the dominant component of terrestrial floras. Frequently angiosperm pollen and leaves account for 60-80% of the species described from Late Cretaceous floras. Understanding the basis for this dramatic change in the composition of terrestrial vegetation during the mid-Cretaceous, and its affects on other elements of the ecosystem (including dinosaurs) is one of the central problems of Mesozoic paleoecology.

TRIASSIC FLORAS AND VEGETATION

Floras of the Triassic are somewhat transitional between those of the Late Paleozoic and the more typical Mesozoic floras of the Jurassic and Early Cretaceous. Only a few Early and Middle Triassic floras have been described and those that are available are mostly from northwest Europe and Siberia and are generally not diverse. Nevertheless, as small as these assemblages are, they show that new kinds of vegetation were beginning to develop. Much more information is available on Late Triassic floras based on several relatively large assemblages from the Late Triassic of southwestern and eastern United States, eastern Greenland, southern Sweden, Siberia, China, southern Africa, South America, and Australia. Although they still contain a few archaic elements that are closely related to Paleozoic taxa, these floras are dominated by many new and novel plants, most of which appear to have originated during the Triassic.

A good example of a diverse Late Triassic flora is that from the southwestern United States. This flora, which includes about 70 species based on megafossils and about 140 based on pollen and spores, is fairly diverse and includes representatives of nearly all major groups of vascular plants, except the angiosperms. It contains a few elements more typical of Late Paleozoic floras, such as certain herbaceous lycopods (e.g., *Chinlea*), large arborescent and small herbaceous horsetails (e.g., *Neocalamites* and *Equisetites*), the supposed cordaitaleans Pelourdea, Samaropsis, and Dadoxylon, and possibly some of the

conifers such as *Brachyphyllum* and *Pagiophyllum*. However, the flora consists mostly of new taxa that are more typical of the Jurassic and Early Cretaceous. The ferns, for example, include species that are closely related to living Matoniaceae (*Phlebopteris*) and Dipteridaceae (*Clathropteris*), and possibly the Gleicheniaceae (*Wingatea*). The true cycads are represented by a pinnate leaf *Aricycas* and the stem *Charmorgia*, both of which show many features of the living taxa. Bennettitalean taxa are particularly abundant in the flora and include the reproductive structure ("flower") *Williamsonia*, as well as leaves that are referred to *Zamites* and *Nilssoniopteris*. Conifers and probable conifer relatives are well represented by many species of *Brachyphyllum* and *Pagiophyllum*, as well as *Pelourdea* and *Podozamites*, and many undescribed cones and seeds. The ginkgo family does not occur in the flora, but is abundant in other Late Triassic fossil assemblages from Siberia and Greenland. Many unusual seed plants also occur in the flora. Some have tentatively been assigned to modern taxa, for instance *Dynophyton* and *Dechellyia* have been compared with living Gnetales, and *Sanmiguelia* has been considered a "preangiosperm" by some authors. However, most of these enigmatic fossil plants cannot be easily accommodated in any living group.

JURASSIC AND EARLY CRETACEOUS FLORAS AND VEGETATION

Jurassic floras occur throughout the world and although they contain a few relict forms related to Paleozoic taxa, they consist principally of plants that developed in the early Mesozoic and are closely related to the living horsetails, ferns, cycads, ginkgos, and conifers. In addition, these mid-Mesozoic floras contain several extinct lineages such as the Caytoniales and Bennettitales. The only major group of land plants that is not known to be present in any Jurassic flora is the flowering plants.

The largest and best known Jurassic floras are those from the Middle Jurassic of Yorkshire, England. These floras have been studied by some of the world's most eminent paleobotanists and include about 200 species based on megafossils that represent nearly all major land plant groups. As a consequence of its size, composition, and diversity, the Yorkshire flora is reasonably representative of most other Jurassic floras and is dominated by "pteridophytes" and Bennettitales, which together comprise nearly half of the recorded species. The "pteridophytes", for example, include 10 horsetails, 30 ferns, and a few other forms. The ferns are particularly diverse and include members of at least six living families, including two that originated in the Paleozoic (Marattiaceae, Osmundaceae) and three that evolved in the early Mesozoic (Matoniaceae, Dipteridaceae, Dicksoniaceae). Bennettitales, which first appear during the Triassic, are represented by a little more than 50 species and thus comprise about one quarter of the flora. Most of the bennettitalean species are based on leaves but the flora also contains many of their flower-like reproductive structures. The true cycads are well represented by about 30 species that include both leaves and reproductive structures. The enigmatic "seedferns" and several other plant groups such as the Caytoniales and Czekanowskiales were also diverse with nine and 14 species respectively. With 14 species the Ginkgoales is also one of the larger groups in the flora, and although most of the species are assigned to the living genus *Ginkgo*, several are assigned to extinct fossil forms. The conifers are represented by about 30 species, many of which can be assigned to modern families, such as the Araucariaceae, Pinaceae, and Taxodiaceae. Other Jurassic floras contain many of the same taxa as the Yorkshire flora, although sometimes in different proportions.

Fossil floras from the Early Cretaceous are very similar in composition to those from the Late Jurassic, particularly at middle and high latitudes. The most extensively studied Early Cretaceous floras are those from northwestern Europe, particularly the Wealden of southern England, Germany, and Belgium.

THE RISE OF ANGIOSPERMS

The most dramatic change in the composition of terrestrial vegetation over the last 200 million years occurred during the mid-Cretaceous with the evolutionary diversification of angiosperms and the associated decline in diversity and abundance of several previously abundant elements in the flora including "cycadophytes" and certain groups of ferns (Figure 4). The stratigraphic diversification of angiosperms is preserved in the fossil pollen record from many parts of the world, but sequences in which the angiosperm radiation can be traced using megafossils (e.g., leaves, flowers) as well as pollen are much less common. The most detailed studies have focused on the Potomac Group of eastern North America, but similar possibilities exist in the Cretaceous of Portugal. In both sequences there is a coordinated and relatively rapid increase in the diversity and abundance of angiosperm pollen grains and leaves that clearly reflects a dramatic change in the composition of terrestrial vegetation.

Fossil pollen grains and leaves that are unequivocally attributable to angiosperms first appear during the Valanginian stage of the Early Cretaceous (c. 140 myr BP). At this stratigraphic level angiosperm remains are much less diverse and abundant than plant fossils of other groups. Relatively quickly, however, in successively younger sediments, the diversity and abundance of angiosperms increases dramatically. At low paleolatitudes (e.g., eastern Brazil, West Africa, the Middle East) angiosperm pollen becomes abundant as early as the Aptian, and by the late Albian and early Cenomanian angiosperm pollen grains and leaves may be locally dominant. By around the end of the Cenomanian (c. 90 myr BP) the presence of several modern families of flowering plants is well documented based on the occurrence of diagnostic fossils. Among these families are the Lauraceae (laurel family), Winteraceae (wintergreen family), Magnoliaceae, Chloranthaceae, Platanaceae (sycamore family), Buxaceae (box family), and possibly Calycanthaceae, Circaeasteraceae, and Himatandraceae.

Quantitative studies of the angiosperm macrofossil and fossil pollen records through the Cretaceous clearly document the magnitude of the extraordinary vegetational change that occurred around 120-110 myr BP, which is comparable in many respects to Late Permian-Triassic and Cretaceous-Tertiary extinction and diversification events in animal evolution. Prior to the Aptian, angiosperms are an insignificant component of both megafossil and microfossil assemblages around the world, but by around the end of the Cenomanian they typically comprise 60% and 30% of species present in megafossil and pollen/spore floras respectively. By the end of the Cretaceous (c. 65 myr BP) angiosperms typically comprise 80% and 50% of species present in megafossil and pollen/spore floras respectively.

Because there are few well-studied Cretaceous megafossil floras from low paleolatitude areas it is difficult to detect any clear geographical pattern to the angiosperm radiation based on the macrofossil data. However, the more abundant information on pollen/spore floras indicates that the angiosperm diversification began earlier, and proceeded most rapidly, at low paleolatitudes. Angiosperm diversification was relatively delayed at

Macrofloras

Others

Conifers

Free-sporing Plants

Angiosperms

Percent

100

80

60

40

20

0

-145   -125   -105   -85   -65

| Neo | B-A | Alb | C | T-S | Cmp | Maa |

Geologic Age

1

Palynofloras

Others

Conifers

Free-sporing Plants

Angiosperms

Percent

100

80

60

40

20

0

-145   -125   -105   -85   -65

| Neo | B-A | Alb | C | T-S | Cmp | Maa |

Geologic Age

2

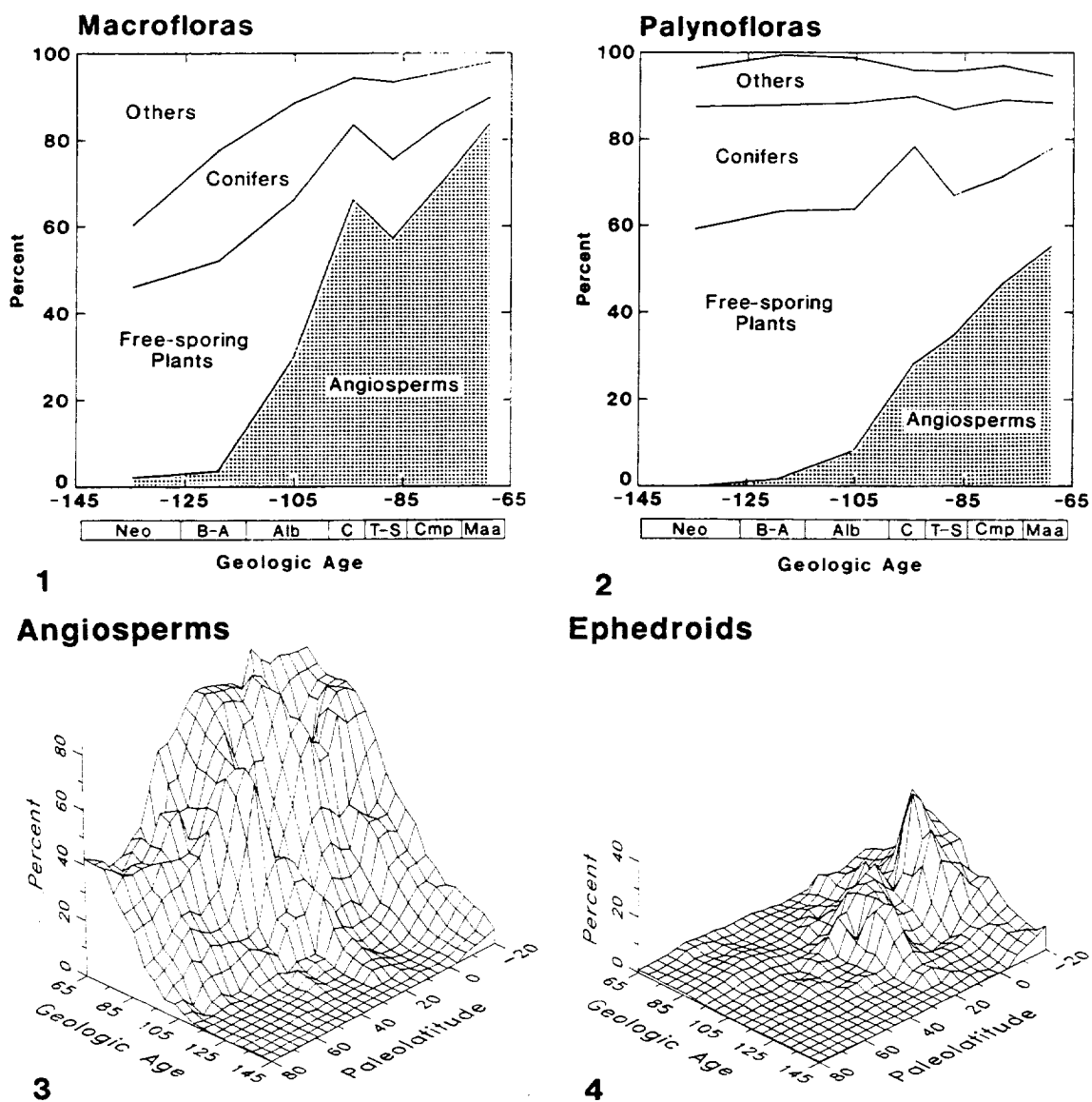## Angiosperms

3

Ephedroids

4

Figure 4--Changing composition of Cretaceous floras. 1-2, comparison of relative diversity of major plant groups based on macrofloras (1) and palynofloras (2). 3-4, temporal and paleolatitudinal diversification patterns for angiosperms (3) and Gnetales (4) (from Crane and Lidgard, 1989).

middle and high latitudes in both the northern and southern hemispheres. Furthermore this pattern persisted, such that by the end of the Cretaceous there was a clear latitudinal pattern in the distribution of angiosperm diversity that mirrors that of today. In the Maastrichtian angiosperms typically account for about 80% of the species in fossil palynofloras from equatorial areas, but only about 40% of the species in palynofloras from high latitude areas.

The underlying basis for this extraordinary change in vegetation during the mid-Cretaceous is unknown. Traditional explanations have focused on potentially advantageous features that angiosperms perhaps possessed that may have allowed them to out-compete, or produce more species than the plant groups that dominated the vegetation earlier in the Mesozoic. For example, it has been suggested that the presence of specialized water-conducting cells (vessels) in angiosperm wood conferred increased tolerance to heat and water stress, and may also have contributed to the origin of large laminar leaves that characterize the group. Similarly it has been suggested that the origin of angiosperm flowers and specific pollination interactions with insects allowed new possibilities for reproductive isolation and perhaps in combination with other features (new modes of dispersal associated with the origin of the angiosperm fruit or improved mechanisms for selecting pollen) allowed angiosperms to accelerate their speciation rate while at the same time reducing their extinction rate. However, recent studies of the fossil pollen record have complicated these angiosperm-centered explanations of mid-Cretaceous vegetational change, and have shown that the Gnetales also diversified at about the same time (Barremian-Cenomanian) and in the same place (low latitudes). This suggests that the ultimate cause of this major vegetational transition may have been environmental change. For example, the mid-Cretaceous was a time of unusually high sea level, unusually rapid growth of mid-oceanic ridges, and perhaps, as a consequence of increased volcanic activity, higher levels of atmospheric carbon dioxide. Such conditions could have potentially favored plants such as angiosperms and Gnetales with weedy life-histories.

LATE CRETACEOUS FLORAS AND VEGETATION

During the Late Cretaceous angiosperm-dominated plant communities can be recognized for the first time that are fundamentally similar in composition to those of today. Numerous Late Cretaceous floras are known from eastern and western North America, as well as from Europe and Asia. Traditionally, most of the available information on these floras has been based on fossil leaves and pollen, but more recently several fossil floras with extremely well-preserved angiosperm flowers have been described. The most thoroughly studied of these is from the Santonian/Campanian of Scania, southern Sweden, which contains flowers, fruits and seeds similar to those of extant groups such as Ericales (heather family), Juglandales (walnut order), Chloranthaceae, Platanaceae (sycamore family), Hamamelidaceae (witch hazel family), and Saxifragales (currant family). Similar floras are also known from elsewhere in Europe and eastern North America (e.g., Neuse River, North Carolina; Allon, Georgia). These floras are dominated by angiosperm remains and clearly document the increasing number and diversity of angiosperm families that can be recognized at progressively younger localities through the Late Cretaceous.

Despite the increasing modernity of Late Cretaceous floras there are reasons to be cautious about direct ecological comparisons with modern vegetation. The possible

Figure 5--Comparison of the Field Museum reconstruction of <u>Archaeanthus</u> (1) with extant <u>Liriodendron</u> (2). Photos courtesy The Field Museum.
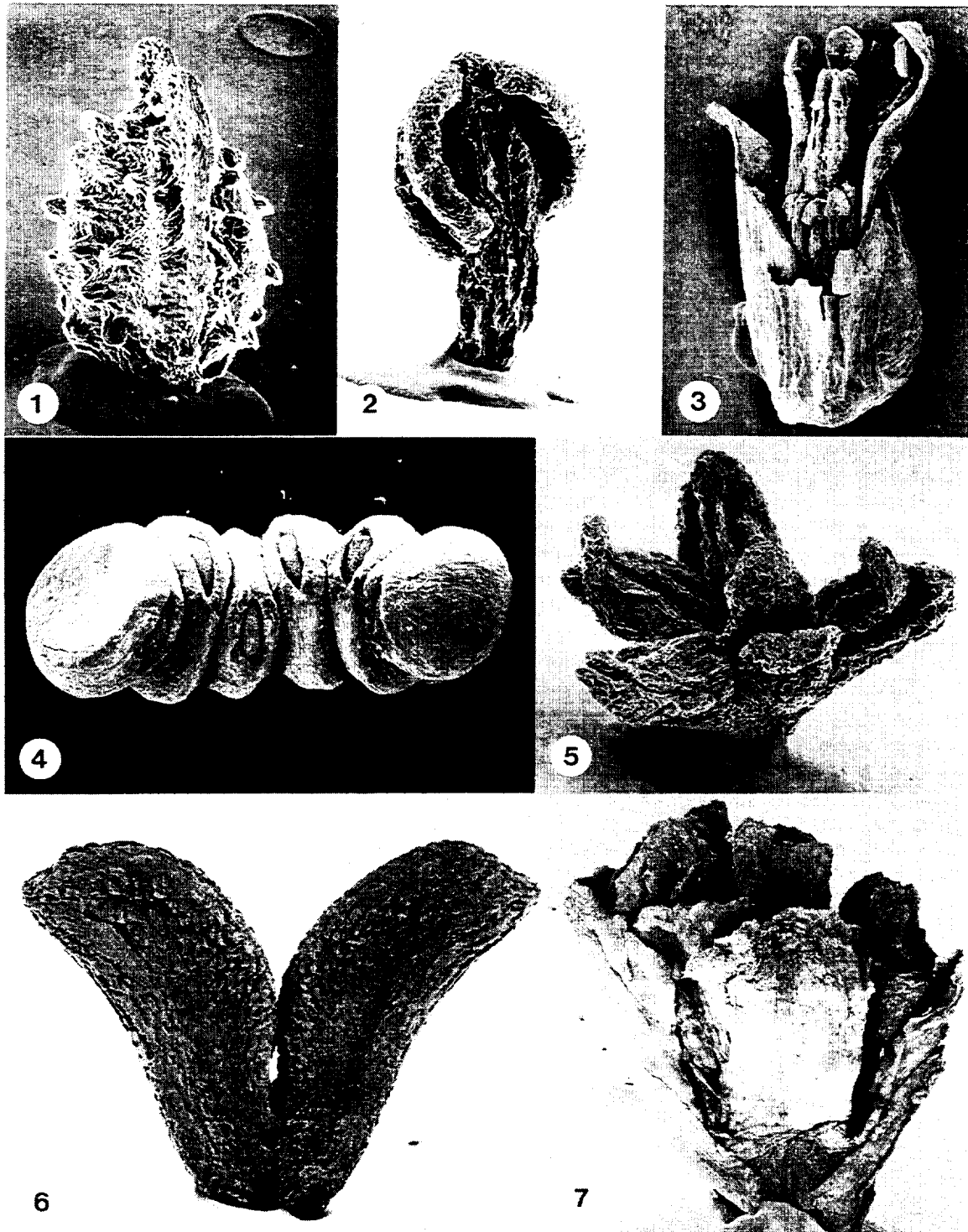
Figure 6--Selection of mid-Cretaceous early angiosperm flowers from the Potomac Group. 1, Couperites mauldinensis, a fruit similar to the family Chloranthaceae, x 60. 2, single dispersed stamen, x 100. 3, Mauldinia mirabilis, a member of the Lauraceae (avocado family), x 18. 4, a group of magnoliid seeds, x 14. 5-6, staminate (5) and pistillate (6) flowers of Spanomera mauldinensis, a fossil plant with affinities to the Buxaceae (box family), x 110. 7, Pistillate flower of Platanocarpus brookensis, a sycamore-like plant, x 44.

ecological effects of large herbivorous dinosaurs need to be considered (see below). Also recent studies of a remarkable *in situ* fossil flora preserved in volcanic ash from the mid-Maastrichtian of Wyoming (Meteetsee Formation) have shown that despite the dominance of angiosperms in terms of their diversity (66%), they account for a much smaller proportion (42%) of the ground cover. At least in the mid-continent of North America, close to the margin of the Western Interior Seaway, the vegetation was a relatively open, fern-palmetto savanna. It is also interesting that some of the angiosperm (dicot) trees (e.g., Platanaceae, Cercidiphyllaceae) that dominate Maastrichtian fossil floras in fluvial depositional environments are a very minor component of this *in situ* flora. There is evidently much more work to be done to build an accurate impression of late Cretaceous vegetation on a global scale.

THE TERMINAL CRETACEOUS EVENT

The terminal Cretaceous event, or Cretaceous-Tertiary ("K-T") extinction, is best known for the demise of the dinosaurs but also involved the loss of many species of marine animals. Although there is ongoing debate concerning the cause (or causes) of this event (e.g., volcanic processes vs. impact of extraterrestrial objects) and the details of the observed extinction patterns, the evidence (high iridium levels, shocked quartz, microtektites) seem most consistent with the occurrence of one, or possibly two, bolide impacts. Evidence from fossil plants shows that vegetational changes at the K-T boundary varied by latitude and geographic region, but are best documented in the western interior of North America. Fossil pollen and leaf assemblages from the latest Cretaceous and earliest Tertiary of this region show a major short-term disruption of the terrestrial ecosystem at the K-T boundary that is reflected in a sudden increase in frequency of a single type of fern spore. The occurrence of this "fern spike" in the palynological record has been interpreted as the first stage of vegetational recovery after a massive ecological disruption, perhaps caused by a relatively brief (c. two month) "impact winter". Ferns are frequently the first plants to recover after a major disturbance such as a volcanic eruption. Following the "fern spike", evidence from fossil leaves suggests that there was a substantial increase in both precipitation and mean annual temperature compared to the climate of the Late Maastrichtian. In terrestrial vegetation, one consequence of these environmental changes in some areas was the apparent extinction of many broadleaved evergreen angiosperms, as well as an increase in the proportion of deciduous taxa.

DINOSAUR-PLANT INTERACTIONS

The existence of dinosaur faunas dominated by large herbivorous sauropods undoubtedly had a significant impact on Jurassic and Early Cretaceous vegetation. These animals were substantially larger than all living herbivores, probably had low metabolic rates, and existed on a diet of plant material with poor nutritional qualities. A considerable amount of plant material would therefore have been needed to sustain these animals. Their rake-like teeth (e.g., *Brachiosaurus*, Figure 7) would have been efficient at stripping leaves from branches, but were not suitable for grinding the food, which would have been processed in a gastric mill. Taken as a whole, the activities of sauropods would have resulted in substantial disturbance in Jurassic and Early Cretaceous vegetation, and their generalized feeding behavior would not have favored the development of specialized animal dispersal mechanisms among contemporary plants.
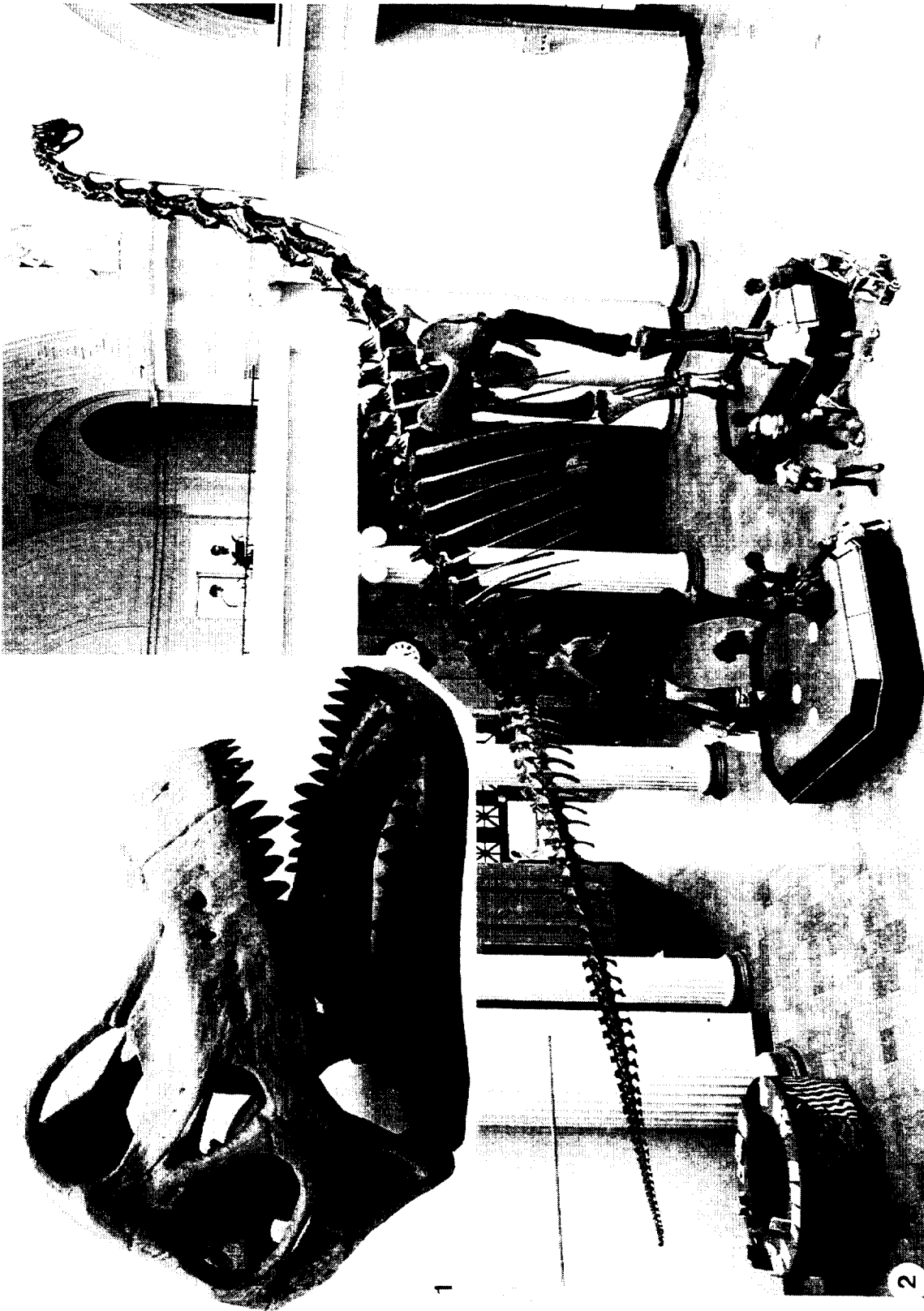
Figure 7.--The Field Museum mount of Brachiosaurus altithorax. 1, detail of skull showing rake-like teeth for stripping branches of leaves. 2, photograph showing whole mount.

These factors may have facilitated the spread of plants such angiosperms with "weedy" life cycles, small generalized propagules and rapid growth rates.

In contrast to the situation in the Jurassic and Early Cretaceous, the dinosaur faunas of the Late Cretaceous were dominated by hadrosaur and ceratopsian ornithopods. These animals are smaller than sauropods, had teeth capable of grinding plant material in the mouth, and were perhaps able to exploit more successfully the higher productivity, more nutritious quality and smaller stature inferred for Late Cretaceous angiosperms. However, throughout the Late Cretaceous disturbance by herbivorous dinosaurs (especially in large herds) would still have been a major ecological factor and some authors have suggested that this was even sufficient to retard the development of closed angiosperm forests. In light of these interpretations the demise of dinosaurs at the end of the Cretaceous was a pivotal factor in the development of more modern ecosystems dominated by angiosperm trees and in which angiosperms exhibit specialized dispersal strategies involving birds and mammals.

Acknowledgements

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Dinosaur Habitats: An Example
from the Late Cretaceous Fossil Forest Study Area,
San Juan Basin, Northwestern New Mexico

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INTRODUCTION

In recent years paleontology has witnessed explosive popularity in schools at all grade levels as well as among the general public. It is ironic that although paleontology continues to receive such interest and attention, teaching and research programs at universities, industry, museums and elsewhere are in decline with fewer positions committed to paleontology and less interest in collecting or storing fossils. Yet, the fact remains that paleontology is a cornerstone of geologic and evolutionary science, as well as having important contributions to make towards discovering and evaluating natural resources. The truths recognized more than a century ago by F. B. Meek and A. H. Worthen (1866), although written in a style that belies its age, are still appropriate:

"When it is therefore borne in mind, that coal and other valuable minerals were not indiscriminately distributed through the earth, but were mainly formed or deposited, at least in quantities and under conditions to be useful to man, during particular geological periods, the importance of knowing to what epoch of the earth's history the rocks of any given district belong, before undertaking mining enterprises of any kind, will be readily understood, and the intelligent general reader will at once comprehend why it is that geologists give so much attention to fossils. In short, the first and most important step in the prosecution of a geological survey, is a careful and thorough study and investigation of the organic remains found in every seam and stratum of the rocks of the district to be explored; for without a knowledge of these, all conclusions in regard to the geological structure of the country, or of the age and position in the geological column of its rocks, must necessarily be vague and unreliable. Indeed, without the aid of Palaeontology, Geology would scarcely be entitled to rank as a science at all."

One of the important derivatives of the recent interest in paleontology has been the opportunity to use paleontology as a vehicle for enhancing science education for both teachers and students. However, because of inadequacies in geology and biology in their own training, science teachers are unable to take full advantage of

young people's enthusiasm for fossils. For more than a decade, I was fortunate to be able to offer a series of summer field and laboratory courses in paleontology. The field paleontology program included on-site participation in ongoing research projects and took place in the rigorous demanding environment of New Mexico's San Juan Basin. In addition to actual paleontological survey, data recording, excavation and transport of a diversity of fossils, teacher-students were exposed to basic geologic and paleontologic principles as well as economic and environmental geology. Parallel laboratory courses enabled participants to learn preparation and conservation methodologies. Students were involved in the preparation and study of specimens that they collected (Chavez and Wolberg, 1988; Wolberg and Chavez, 1993). Of course, the richness of the Fossil Forest Study Area, discussed below enhanced the experience.

ANCIENT WORLDS

One of the most fascinating aspects of paleontology is attempting to address the questions of what the world or some small part of it looked like in the past, what animals and plants were alive, what the landscape looked like and what kind of climate prevailed. The paleontologist is able to find information in the fossil bones, traces of animals or their activities, shells, wood and leaves that are found in the rocks. The rocks themselves provide information in the kind of layering, composition and mineralogy, size and shapes of the particles comprising them, and even trace elements. Because there are so many variables that determine what will be preserved in the rocks of the Earth, most often paleontologists only have enough information available to provide a partial answer to these questions. For example, fossils may have been transported, damaged and only incompletely preserved or the rock record is incomplete; gaps representing varying durations of time almost always exist in any sequence of rock layers.

Every now and then, however, sites are discovered where a great deal of information is available. Relatively recent research indicates that rock sequences may also contain biochemical fossils and geochemical information that considerably enhances our understanding of a part of the past. The Fossil Forest Study Area of the San Juan Basin of New Mexico described below is an unusual area where an abundance and diversity of data is available that provides a glimpse of dinosaur habitats that existed in this part of the world about 72-74 million years ago. The Fossil Forest also provides insights into early Twentieth Century fossil collecting activities, geological investigations, and land use patterns (Wolberg and Bellis, 1990).

LATE CRETACEOUS DINOSAURS IN NEW MEXICO

New Mexico is a state richly endowed in cultural history, scenery, geology and paleontology. Late Cretaceous rocks are best documented in the San Juan Basin of northwestern New Mexico, the Raton Basin of northeastern New Mexico and the area in and about Elephant Butte Reservoir, near Truth or Consequences, in south-central New Mexico. Unfortunately, in spite of an abundance of fossils, the geologic section in the San Juan Basin is not continuous through the Cretaceous into the Tertiary. Although a continuous section is present, to date evidence of dinosaurs in Late Cretaceous rocks in the Raton Basin seems to be restricted to footprints (C. Pilmore, pers. com.). Early in this century, construction of the Elephant Butte Dam and Reservoir led to reports of dinosaur bones in rocks in the area. The field mapping work of then graduate student Richard Lozinsky resulted in the rediscovery of a fairly diverse dinosaur fauna of latest Cretaceous (Maastrichtian) age (Lozinsky and others, 1984; Wolberg, Gillette and Hunt, 1986; Gillette, Wolberg and Hunt, 1986). Since then, continued studies by G. Mack has led to additional significant discoveries of dinosaurs and plant fossils. Mack is preparing what will be the definitive publication on the McRae Formation, but to date, the stratigraphy needs to be better delineated.

Thus, the Cretaceous paleontology of the San Juan Basin is much better known than other parts of the State, if only because of the abundance of rocks, fossils and researchers interested in finding those fossils. In part this documented record is the result of a dry climate, poor plant cover and consequent rock exposures. The Raton Basin has better developed vegetation and more restricted rock exposures. Elephant Butte is now a reservoir, the rocks are under varying amounts of water, and it is only in the last decade that the area has been restudied.

LOCATION AND SETTING

The Fossil Forest study area is located in the west-central part of the San Juan Basin. The largest regional population center, Farmington, lies about 35 miles to the north, and Chaco Canyon, famous for its archeological ruins, lies to the south. The Bisti Badlands, part of which are now included within a Wilderness Area are to the northwest (Figure 1). The Fossil Forest study area occupies parts of Sections 13, 14, 22, 23, 24 of and 26, T23N, R12W. Most of the land is managed by the U. S. Bureau of Land Management and the area is designated as a Research Natural Area (RNA). Reaching the area is possible via NM 44 and then west from the old Huerfano Trading Post, or from NM 370 and then east on County Road 7500.

The Fossil Forest is drained by tributaries of Coal Creek, itself a tributary of De-na-zin, a Navajo term referring to pictoglyphs found nearby;De-na-zin itself is a tributary of Chaco wash. The area is characterized by well developed
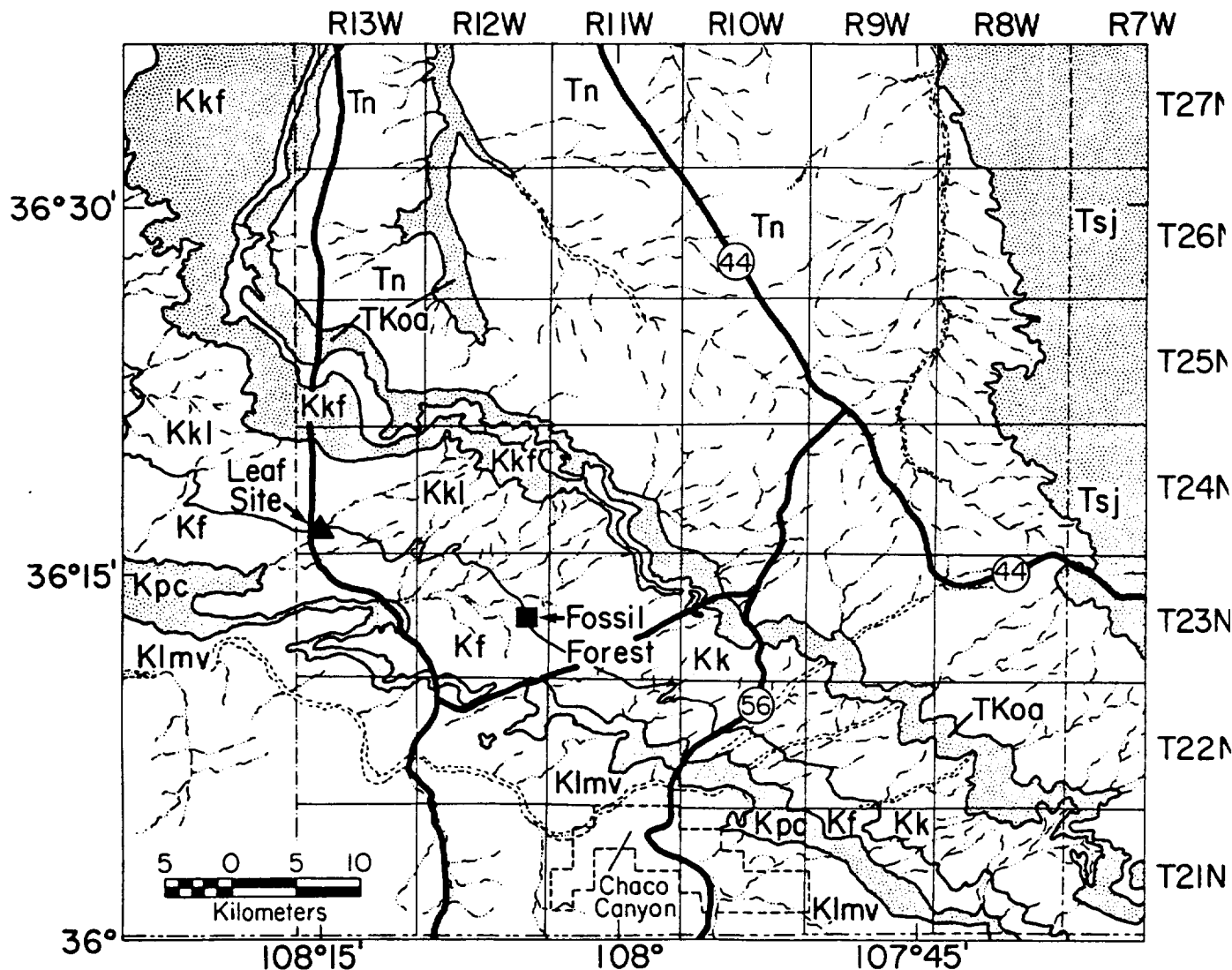
FIGURE 1.--Index and geologic map of the Fossil Forest Study Area in relation to major landmarks. The fossil leaf locality of Robison, Wolberg and Hunt (1982) in the Bisti Badlands is also shown. Abbreviations of rock units from highest to lowest are: Tsj, San Jose Formation (Eocene); Tn, Nacimiento (Paleocene); TKoa, Ojo Alamo (variously Cretaceous or Paleocene); KkF, Farmington Sandstone Member of the Kirtland Shale; Kkl, lower shale member of the Kirtland Shale; Kk, undifferentiated Kirtland Shale; Kf, Fruitland Formation; Kpc, Pictured Cliffs Sandstone; Klmv, undifferentiated Lewis Shale and Mesaverde Group. (After Wolberg and others, 1988) .

badlands topography that provides excellent exposures of the Upper Cretaceous Fruitland Formation and patches of the lower part of the overlying Kirtland Shale. Badlands development is a relatively recent phenomenon related to Holocene base-level lowering (Welles, 1983). The region is situated at an altitude about 6000 ft and the climate is semi-arid. At Chaco Canyon to the south a 35 year record indicates that mean annual precipitation is just slightly less than 9 in/yr, most of which falls between July and October (Gabin and Lesperance, 1994). Temperatures vary greatly with the seasons and even during the course of a day; our field group has recorded a 132 degree fahrenheit air temperature during one July afternoon. But that same evening, 63 degrees fahrenheit was recorded, a temperature range of 69 degrees in one day.

THE ROCKS

The rocks that are exposed in the Fossil Forest were first described as part of a report by Bauer and Reeside (1920). More recently, the stratigraphy has been discussed at length in Wolberg and others (1988) and Wolberg and Bellis (1992). All the rocks that are exposed in the Fossil Forest, except the uppermost capping sandstone discussed below, are included within the Fruitland Formation. The Fruitland Formation, named for outcrops of rock found near the town of Fruitland, New Mexico, west of Farmington, overlies the Pictured Cliffs Sandstone and underlies the Kirtland Shale. The Pictured Cliffs Sandstone is a beach and nearshore marine sandstone that was deposited as the Late Cretaceous sea retreated from the region. Fruitland Formation coals, mudstones, siltstones and sandstones were deposited landward of the Pictured Cliffs sandstones. During the Late Cretaceous, the Fossil Forest was situated very near the shore of the Cretaceous sea which split the North American continent into separate island continents (Figure 2). Of some interest as well is the fact that the Fruitland Formation contains more than 90% of the coal resources and most of the coal bed methane found in New Mexico. The coal rich regions of New Mexico, especially the San Juan Basin are economically dependent on energy development. The history of mining has been cyclic and generally tied to other economic and social factors(Anderson and Wolberg, 1987). The geology and fuel resources of the Fruitland Formation were discussed at length in Fassett and Hinds (1971).

Our research in the Fossil Forest required an understanding of which rock layers were in the area. In order to build up a complete picture, several rock sections were described and thicknesses measured. The resulting compilation of this data is shown in Figure 3. The composite rock sequence begins with a purple ash bed above which is a major coal that has a mudstone parting rich in fossil leaves. A second plant layer caps this coal and is also rich in fossil leaves and consists of a poor shale; this rock unit is partially covered and when it reappears, it underlies still another coal.The top of this coal layer is split by repeated
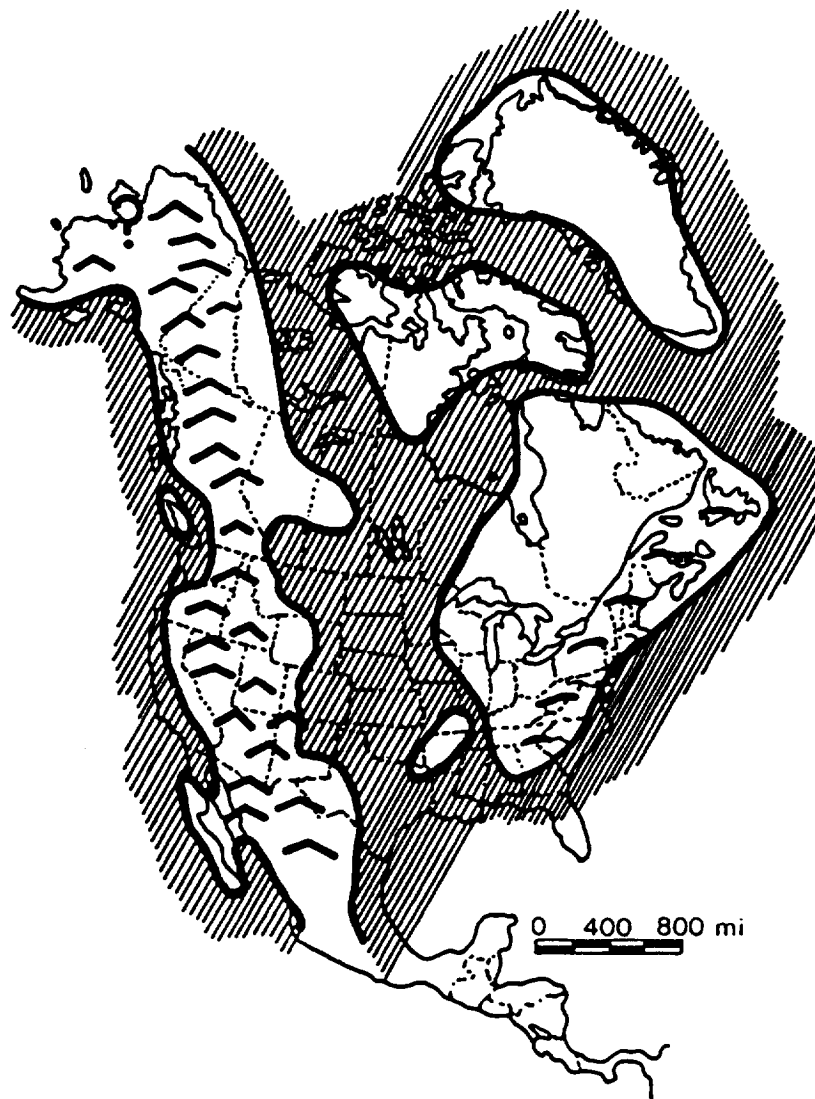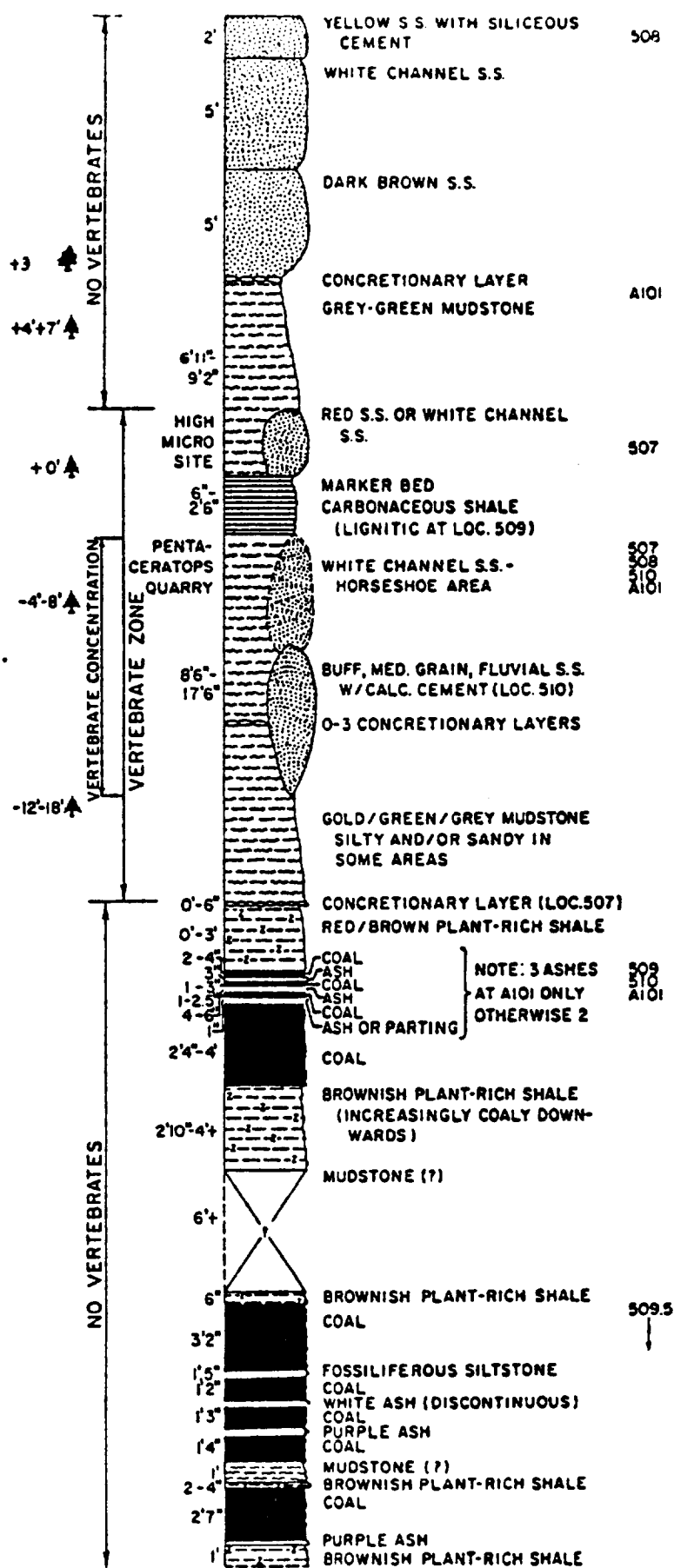
FIGURE 2.--North American paleogeography during Early Maastrichtian time. The Fossil Forest in northwestern New Mexico was situated just at sealevel. The sea withdrew to the northeast. (After Williams and Stelck, 1975).

FIGURE 3.--Composite strati-
graphic section for rocks
exposed in the Fossil For-
est. Five tree stump hori-
zons are shown and these
are separated by at least
three fossil leaf horizons.
The numbers on the right
correspond to individual
measured sections used to
build up the composite
section and include Bauer
and Reeside (1920) re-
measured sections. The
"High Micro Site "has pro-
duced dinosaur egg shell
fragments and is at about
the same level as the in-
fant hadrosaur locality.
Note that vertebrate fos-
sils occur in a relatively
restricted stratigraphic
zone. (After Wolberg and
others, 1988).

NO VERTEBRATES

+3 ♠
+4'+7' ♠

+0' ♠

HIGH
MICRO
SITE

PENTA-
CERATOPS
QUARRY

-4'-8' ♠

VERTEBRATE CONCENTRATION
VERTEBRATE ZONE

-12'-18' ♠

NO VERTEBRATES

2'
5'
5'

6'11"-
9'2"

6"-
2'6"

8'6"-
17'6"

0'-6"
0'-3'
2-4"
1-3"
1-2.5"
4-6"

2'4"-4'

2'10"-4'+

6'+

6"

3'2"

1'5"
1'2"

1'3"

1'4"

2-4"

2'7"

1'

YELLOW S.S. WITH SILICEOUS
CEMENT   508

WHITE CHANNEL S.S.

DARK BROWN S.S.

CONCRETIONARY LAYER
GREY-GREEN MUDSTONE   A101

RED S.S. OR WHITE CHANNEL
S.S.   507

MARKER BED
CARBONACEOUS SHALE
(LIGNITIC AT LOC. 509)
                                 507
WHITE CHANNEL S.S.-   508
HORSESHOE AREA   510
                                 A101

BUFF, MED. GRAIN, FLUVIAL S.S.
W/CALC. CEMENT (LOC. 510)

0-3 CONCRETIONARY LAYERS

GOLD/GREEN/GREY MUDSTONE
SILTY AND/OR SANDY IN
SOME AREAS

CONCRETIONARY LAYER (LOC.507)
RED/BROWN PLANT-RICH SHALE
COAL
ASH
COAL   NOTE: 3 ASHES   509
ASH   AT A101 ONLY   510
COAL   OTHERWISE 2   A101
ASH OR PARTING

COAL

BROWNISH PLANT-RICH SHALE
(INCREASINGLY COALY DOWN-
WARDS)

MUDSTONE (?)

BROWNISH PLANT-RICH SHALE   509.5
COAL

FOSSILIFEROUS SILTSTONE
COAL
WHITE ASH (DISCONTINUOUS)
COAL
PURPLE ASH
COAL
MUDSTONE (?)
BROWNISH PLANT-RICH SHALE
COAL

PURPLE ASH
BROWNISH PLANT-RICH SHALE

volcanic ash partings--no less than three are present. This layer is in turn followed by another plant-rich shale which gives way to a green to gray mudstone.

This last mudstone is interesting because the first of the tree stump and log layers appears in this rock layer and because just about all of the vertebrate fossils found in the Fossil Forest first appear in this layer. The mudstones are frequently channeled, cut out and replaced by stream channel sandstones, or at two localities by sandstones containing marine fossils indicating that the sea briefly invaded the area at least twice. This whole interval ends with a thin coaly shale that forms a key marker bed throughout the study area.

Above this marker bed, another mudstone occurs that is also frequently cut out and replaced by channel sandstones. Just above the base of this mudstone, vertebrate bones and teeth disappear, although at least two more layers of tree stumps and one layer of fossil leaves can be found. This mudstone is capped by a sequence of brown weathering, white and yellow sandstones, respectively. The yellow sandstone, the highest sandstone in the area, has a siliceous cement, unlike all the lower sandstones that have a carbonate cement. The entire stack of rocks exposed in the Fossil Forest is no more than 75 feet thick.

As noted above, the Fruitland Formation lies above the Pictured Cliffs Sandstone; the nearest place the Pictured Cliffs is exposed in the region is more than 10 miles to the northwest. We knew that the Pictured Cliffs could be encountered at some depth below the surface in the Fossil Forest. Fortunately, the opportunity arose to drill a hole and retrieve a continuous core, the actual rocks that the drill went through in its passage through the Earth. A total of 303 feet were drilled through and except for the uppermost 15 ft or so of windblown sand all of the rock core was recovered. This core provided a complete record of rocks preserved in the area-the 75 feet of rock exposures fits somewhere in the 300 feet of the drill core. We placed the contact between the Pictured Cliffs and the Fruitland Formation about 45 feet above the bottom of the core, or at 258 feet. Thus the 75 feet of the rocks exposed in the study area must lie within the upper 258 feet of the core. As discussed elsewhere, the core has been sampled for a number of reasons including trace elements, clays, and palynology.

WHAT'S IN A NAME

The Fossil Forest is named for the occurrence of numerous fossil tree stumps and logs; almost all of the stumps are in situ, they are found where they actually were in life. The stumps and logs do not all occur at the same level. Instead, at least five different levels of trees can be recognized, each separated by thicknesses of rock, and each representing a different forest that occupied the area. Still more interesting is the fact that five fossil leaf horizons have been found as well. Two of these are below the lowest stump horizon and three are found between layers

that have tree stumps and logs. These leaf layers must represent still other forests that existed in the area and, in all, at least eight different forests are preserved in the Fossil Forest Study Area. We have recognized at least three tree stump levels in the Bisti Badlands area separated by two leaf horizons (Robison and others, 1982). These are high in the section and almost certainly are equivalent to some of the Fossil Forest horizons.

Sediments frequently contain microscopically-sized fossils such as pollen grains and spores. These can be very useful as "index fossils" that provide information about the age of the rocks in which they occur, as well as information about the kinds of habitats that existed. Our research group has sampled the exposed rock layers at regular intervals for these fossils as well. We have preliminary results (Jameossanaie, Wolberg and Bellis, 1990) and analysis of the material continues under the direction of Aureal Cross, Michigan State University.

All of these fossils are plants of one kind or another and, as must be apparent, the Fossil Forest provides an abundance of fossil plant material for study. We have identified several kinds of trees from the petrified wood stumps and logs: most of the stumps and logs in the an area we have called, "the main stump field," are of cypress-like trees and a stand of palm trees. Elsewhere, we have discovered other palm trees and, still elsewhere, we have discovered pines and redwoods. These identifications have been made by paleobotanists who studied the fine structure of the wood. The leaves and some seeds have also been identified. Table 1 lists the fossil plants identified in the Fossil Forest. We have mapped the occurrences of stumps and logs in the main stump field (Figure 4). In all we located more than 400 stumps and 40 logs (Wolberg and others, 1988). Three forest levels are located in the main stump field. Using the carbonaceous shale marker bed, we were able to accurately locate the highest forest just above the marker bed; the next lower level is 4-8 feet below the marker bed and the lowest forest is 12 to 18 feet below the marker bed. Most of the logs are associated with the intermediate forest level. The logs seem to show a preferred orientation of their long axes with a NE-SW trend. Many of the stumps show evidence of rapid burial, while others have rotted cores indicating a period of exposure and decay before final burial.

Also present in the rocks are bits and pieces of fossil resin, amber. This material is fascinating for many reasons. Resins are secreted by many different kinds of plants and essentially serves a protective function. When just exuded, the resin is viscous and flows and as it flows, it engulfs bits and pieces of organic material and even whole organisms in the path of the flow. Almost everyone is familiar with insects preserved in amber but in fact, whole frogs and even an occasional lizard has been so preserved. Less well known is the fact that pollen grains, spores, and even single-celled organisms may be trapped in amber. It appears that resins also trap little pockets of air and even water. Thus, it seems probable that pockets of ancient atmosphere are preserved in amber. Once
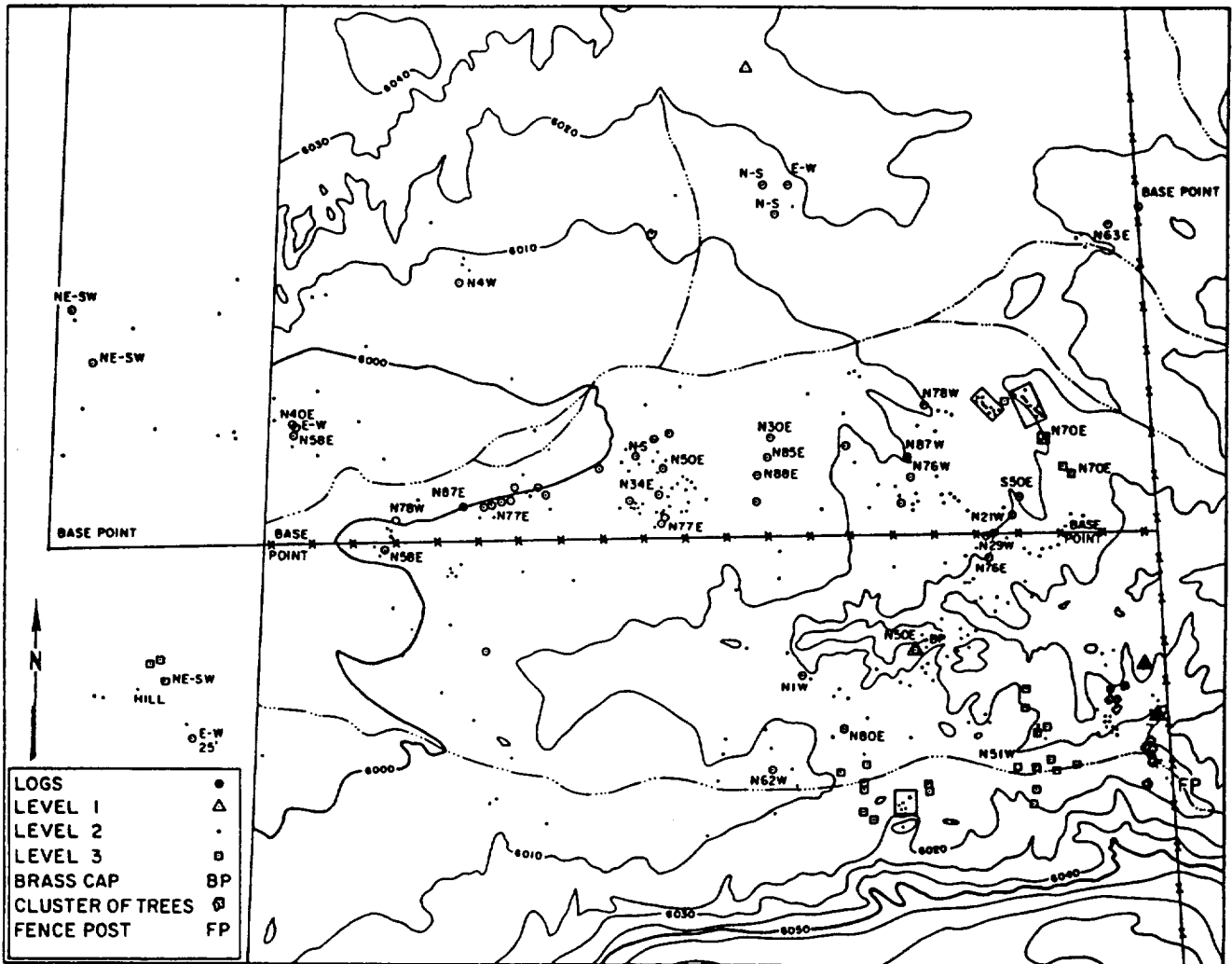
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FIGURE 4.--Distribution of fossil tree stumps and logs in the "Main Stump Field"
Fossil Forest. More than 400 trees have been plotted in this area and three
forest levels are present. The fence lines date from the late 1930's after the
passage of the Taylor Grazing Act; they were probably supposed be N-S and E-W
but are just off true from an original base to the south, off the map. (After
Wolberg and others, 1988).

hardened, resins are quite resistant to weathering and are generally insoluable.

The opportunity to study such a complete record of environments through time from outcrop and core encouraged us to sample the rocks for trace elements and clays. Using x-ray analysis and in some cases scanning electron microscopy, we analyzed the rocks for Mg, Mn, Co, Pb, Be, Ni, V, Cr, Cu, Au, Fe and Zn. The kaolinitic clays seen in the core were originally Na-smectite rich ashes. Of interest, we happened to discover in the core repeated levels where the unusual double carbonate mineral, huntite, was present. Previously, huntite was only known from late Quaternary localities, including the Persian Gulf. Huntite is an indicator of periodic warm, arid conditions. Proprietary oil company drill data across the San Juan Basin has verified our discovery and is now used to indicate mineralogical marker horizons. It seems clear that the Fruitland is characterized by repeated episodes of marine incursions and climatic variation from warm humid to warm arid.

SHELLS, TEETH AND BONES

In addition to fossil plants, the Fossil Forest study area contains an abundance of fossil animal remains. Among these, several kinds of snails and clams have been recovered and are presently being studied by Joseph Hartman, a paleontologist with special expertise in freshwater mollusks. Hartman (1981) noted that brackish water mollusks predominate in the Pictured Cliffs Formation and the lower part of the Fruitland Formation. In general, from the lower part of the Fruitland Formation upward, freshwater mollusks become more important in the record.

There are exceptions to this trend, however, and these are of some significance in understanding the history of the area. During the 1990 and 1991 field seasons, we discovered two localities, one between the second and third forest levels, and another locality just below the fifth forest level, which had marine mollusks preserved. At the lowermost locality we found a partial ammonite cephalopod shell and large marine bivalves. At the second locality we discovered a marine gastropod and other bivalves. These occurrences indicate to us that the sea returned to the area at least twice, and these marine transgressions seem to be the latest incursions yet identified in the San Juan Basin. These incursions of the sea were followed by withdrawals that exposed larger areas of land again, and allowed for the return of lost terrestrial habitats.

One of the more interesting sidelights of our research in the Fossil Forest centered on a number of tree stumps that apparently had rotted cores that had been filled with sediment. We removed and broke down the silty mudstone filling from three of the stumps, sifted the resulting material and examined the residue under a low powered microscope. Fossil material was scarce but significant and

consisted of three isolated garfish scales and two larval caddis fly cases. Caddis flies have an aquatic larval stage and this information together with the gar scales indicate that the Fossil Forest was submerged by freshwater for an extended period of time, certainly long enough and deep enough to fill the rotted stumps, have gars swimming about and habitats suitable for insects with an aquatic stage in their life cycle. The discovery of the caddis fly cases was the first record of Cretaceous insects in the Southwest (Wolberg and others, 1988).

The Fossil Forest would be interesting if it only preserved the geology and the plant fossils and the rare insect remains or occasional fish scales that are found there. However, many other kinds of fossils occur in the Fossil Forest. Table 2 lists the vertebrate fossils that have been identified from various localities and includes fishes, amphibians, lizards, turtles, crocodilians, dinosaurs and mammals. In addition to gars, sharks, rays and batfish occur, emphasizing the proximity to the sea.

Hall and Wolberg (1989) described an incomplete skeleton of a new, very large amiid, *Amia? chauloideia*. This very interesting fossil was the only specimen that occurred in a greenish-gray mudstone overlying the lowest level of stumps in the main stump field. The mudstone was lens-like and no more than approximately 5 feet thick and 75 feet in length; it may represent a filled ox-bow. This new species seems to have a wide distribution through the Fruitland Formation, a fact that was previously unrecognized.

The most common and widely distributed animal remains in the Fossil Forest are turtle shell fragments--although complete or partially complete turtle material is rare, bits and pieces of eroded turtle shell are resistant and persistently occur over a wide area of the Fossil Forest and elsewhere in many areas where Fruitland and Kirtland rocks are exposed in the San Juan Basin. Some diversity of the turtle fauna is evident in that at least four different genera have been identified by admittedly crude methods; the turtles have not been studied in detail. The same can be said for the crocodilian fossils found but three different kinds have been recognized.

The mammals, however, have been studied in detail (Rigby and Wolberg, 1987; Wolberg, 1992a). The Fossil Forest is exciting because it has provided the best glimpse of what mammals were like in the Cretaceous of the Southwest. These little animals--almost all were somewhere between a mouse and squirrel in size-- scurried about no doubt trying to be as inconspicuous as possible. During our early work in the Fossil Forest, we conducted our studies in cooperation with field crews of the U. S. Bureau of Land Management. We located the site that was to become our "Quarry I" mammal site and began the tedious process of preparing the material. The rock matrix of Quarry I is basically a clay-pebble conglomerate, the clay pebbles being rip up clasts redeposited in a stream channel. Clay pebbles and any other particles roughly the same size as the pebbles were torn up as mud

clasts and dragged along by the water flow. As the energy of the water diminished, the pebbles and other debris were deposited at the bottom of the channel and covered by finer material.

There is no easy way to study this material; the fossils are distributed randomly through the rock and occur almost entirely as isolated teeth and bone fragments. We had to dig and pry blocks of rock which were then packed in burlap sacks and loaded onto our trucks. We hauled these sacks, some of which weighed more than 100 pounds, back to the laboratory in Socorro, about 250 miles away (or to Albuquerque in the case of material processed by the BLM). I would estimate that we and the BLM crews probably removed at least ten tons of rock from Quarry I.

Removing the rock matrix was only the beginning; once we hauled the rocks back to the lab, the rock matrix was soaked in large drums to which water and a standard laboratory detergent had been added. This had the effect of reducing the matrix in the drums to a slippery, muddy sludge within 24-36 hours. The sludge was then poured onto screens, repeatedly rinsed in a stream of clean water, and the accumulated residue dried. The dried residue was then looked at spoonful by spoonful under a binocular microscope and any interesting material was removed. This drudge work did pay off: every now and then, a spoonful of residue would produce a freshwater fish tooth, scale or shark tooth as well as bits of shell or tiny pieces of amber. More rarely, a mammal tooth fragment or, still more rarely, a relatively complete mammal tooth was discovered. This method of study serves well but has drawbacks. The most important of these is the fact that most of the material recovered will consist of isolated fragments. The process of soaking, washing and drying tends to damage fossils so a tiny jaw that had teeth still in place would end up as separate isolated teeth and an edentulous jaw. Of course, we most likely would never see the jaw or even isolated teeth in the pieces of matrix.

Despite the comparative rarity of teeth, Quarry I proved to be the most productive Cretaceous mammal locality yet discovered in the region and more than compensated us for the work required. Many new species of mammals, as yet known only from the Fossil Forest have been described and named, entirely from isolated teeth. For most mammals, teeth are marvelous structures. Teeth are composed of apatite, a very tough and resistant mineral. Most mammals (and other toothed animals) have many teeth in their mouths and once the animal dies, its teeth stand a better chance of surviving than other parts of the skeleton. Moreover, in the case of molars especially, the complex pattern of cusps and crests have proven to be unique for each species and allow for the formulation of ideas about mammal evolution and interrelationships.

Until we discovered mammals in the Fossil Forest, Cretaceous mammals in the region were known only from teeth. Finally, a chance look at a block of matrix we

were going to soak led to the discovery of a large part of a mammal femur, or thigh bone. The femur proved to be rather distinctive and belongs to a multituberculate mammal, an archaic group of early mammals, now extinct, and especially characterized by unique kinds of teeth. This was and still is the only non-tooth part of a Cretaceous mammal known from the region.

A second mammal locality, uncreatively named by us as Quarry II, has been less intensively worked. This locality is a bit more complex in that although pebble conglomerates do occur, the locality also contains very large freshwater mollusks in some abundance. The shells of these are whole and intact; they are not opened or fragmented. This would indicate that they had not been transported too far before they settled to the bottom of the channel in which they occur.

As noted above, multituberculates were found in the Fossil Forest. A large portion of mammals recovered are marsupials, animals related to and in life very much like the modern opossum, but smaller. Insectivores, very shrew-like in appearance and probably in behavior also occur as a dominant element of the mammal fauna. It is very likely that these mammals tried to keep out of the way of the dinosaurs, large and small, crocodiles, whatever birds may have been present, and probably each other. They were probably nocturnal in habits. The multituberculates were probably exclusively vegetarian, eating fruits, nuts and possibly leaves. The marsupials were most likely culinary generalists, eating just about anything they could find, animal or plant. The "meat-eaters" of their time, the insectivores, no doubt found an abundance of insects as food, but probably would take any small amphibians or reptiles that came their way. They may have eaten any eggs they could find and served as scavengers of carrion.

FOSSIL FOREST DINOSAURS AND DINOSAUR QUARRIES

Dinosaur bones occur in the Fossil Forest. The distribution of these has proven to be of interest. Dinosaur bones (and the preponderance of vertebrate fossils) do not occur uniformly through the geologic section in the Fossil Forest. We have found no fossils below the mudstone just above the uppermost thick coal, or above the highest mudstone in the area. Thus, only about half the exposed rock section contains vertebrate fossils. Most of the vertebrates are associated with channel-form sandstones, generally as a lag deposit within the channels. Exceptions have been found and include perhaps the two best preserved vertebrate fossils we have found and recovered. The first was the new amiid fish described above, which was found in a mudstone. The second discovery was an incomplete skeleton of *Pentaceratops*, found in the fine-grained portion of what we determined was an overbank deposit. This specimen was the second most complete dinosaur (perhaps 50%) of the animal, we ever recovered from the Fossil Forest.

It has been our experience that stream channels are generally not good places for the recovery of articulated fossils. Certainly dinosaur material is abundant in the Fossil Forest channels, but mostly as isolated limbs, portions of limbs, vertebrae, skull fragments or other "stray parts." Early on in our studies, we were able to recover a very nice six-foot long articulated section of hadrosaur tail. Elsewhere, we recovered a series of hadrosaur vertebrae, again in a channel sand. We really never relished working in the sandstones. Most of the sandstones proved to be extremely hard, much like concrete if not harder. Similarly, probably because of its compactness, these sandstones tended to split in a random way, frequently across and not along a bone. We dealt with the hardness of the material by utilizing hand-held, air driven impact hammers as well as a more conventional jack-hammer. Once again, this created logistical problems. The rough, broken nature of the topography means that everything must be carried or dragged into the quarry areas. By the same token, any excavated blocks have to be hauled out.

One of our crew, Carol Horton, stumbled upon a series of obvious rib ends poking out of a channel sandstone at about ground level. Additional probing with hammer, chisel, awl and brushwork indicated that the ribs continued into the matrix and additional bones were associated with the ribs. Carol reported the discovery and others were assigned to continue to remove overburden; the sandstone was especially hard. As we probed it became more and more apparent that we were dealing with a single, most likely articulated and very large dinosaur, certainly more than 25 feet in length, laying approximately parallel to the axis of the stream channel. The crew moved more and more matrix, interestingly exposing a very large fossil log, also laying parallel to the axis of the channel and the dinosaur. This log eventually proved to be a redwood; it also preserved a number of features that were rather significant.

Firstly, the log is simply massive and also seemed to retain a large number of branches with leaves preserved as a carbonized halo still visible in the sandstone matrix. A large portion of the log that we exposed (but not all) appeared to be not just carbonized, but burnt. Other parts of the log were unaffected by charring and were silicified. Further, the dinosaur skeleton appeared to be associated with the log. The most reasonable hypothesis indicated that the redwood log had snagged the dinosaur carcass and prevented it from being dragged further along the channel and disarticulated. Burial must have been rapid, again because the skeleton remained articulated and the branches and leaf halo of the tree were preserved. Continued excavation of the locality, now grown into a major quarry, uncovered an intact humerus, upper arm, more than four feet in length. The skull, if present, must be still be within the hill; both femurs are present and are still buried.

The very large size of this specimen was unexpected. About the same time we were working at this new quarry, our attention was directed elsewhere, some miles

TABLE ONE
FOSSIL PLANTS IDENTIFIED FROM THE FOSSIL FOREST

Ferns: *Dryopteris, Equisetum*

Conifers: *Araucaria, Taxodium, Sequoia*

Monocots: *Potamogeton*? (an aquatic plant); Sabalites (a palm)

Dicots: *Salix, Populus, Dryophyllum, Ficus, Polygonum, Rumex, Plantanus, Laurophyllum*

Others: *Viburnum, Podozamites*

TABLE TWO
FOSSIL ANIMALS IDENTIFIED FROM THE FOSSIL FOREST

Invertebrates:

Several species of freshwater and marine clams and snails, a marine cephalopod and an insect

Vertebrates:

Sharks and rays: *Lissodus, Myledaphus, Ischyrhiza, Ptychotrygon*

Boney fishes: *Amia, Lepisosteus, Paralbula*

An unidentified salamander

An unidentified lizard

Turtles: *Baena, Adocus, Aspiderites, Trionyx*

Crocodiles: *Brachychampsa, Crocodylus, Goniopholis?*

Theropod dinosaurs: an unidentified coelurid; Albertosaurus

Ornithopod dinosaurs: *Hadrosaurus ("Kritosaurus");Parasaurolophus;* an ankylosaur; *Pentaceratops*

Mammals:

Three different multituberculates

Marsupials: *Alphadon* (three species); *Ectocentrocristus; Pediomys* (two species); *Aquiladelphis; Eodelphis*

Insectivores: *Gypsonictops* (two species); *Cimolestes, Paranyctoides*

to the northwest. There, fortune truly shined for we managed to excavate, quite by chance the first dinosaur footprints reported from the San Juan Basin (Wolberg, Hall and Bellis, 1988). The largest and most complete print was truly huge, more than 2.5 ft in diameter by the time we completed our excavation. The print was made by a hadrosaur, probably about the same, size as the Fossil Forest beast.

Of great interest, and unexpected, was the discovery in the quarry of preserved dinosaur skin (Hall, Wolberg and West, 1988). The skin occurs several feet above the skeleton and does not appear to be directly associated with it. It occurred as sections of sheet-like material tightly folded over in several layers. In cross-section, the skin can be seen to consist of sqamation that is tubercular and non-imbricated. Most likely, for whatever reason, sheets of dinosaur skin, possibly shed, ended up tangled in the same tree that snared the skeleton.

Table 2 also lists the dinosaurs that have been identified in the Fossil Forest. Dinosaur bones are not rare in the Fossil Forest. Few kinds of dinosaurs have been identified, but certainly at least 50 individuals are represented. Even in this limited sample, it is apparent that hadrosaurs are the most common form followed by ceratopsians. *Albertosaurus* teeth are not uncommon, but skeletal material is rare; we may have discovered one tibia. The ankylosaurid we discovered, known only from armor, is the only such form found.

We realized right from the start that we were not the first group to excavate in the Fossil Forest. A number of quarries are present within the study area, several of substantial size. However, we were not able to document any reported fossils from the study area in any institution. This prompted a bit of detective work into land use history, land management agencies, fencelines, Native Americans, trading posts and old roads (Wolberg and others, 1988). It turns out that the fence lines in the Fossil Forest originate with the passage of the Taylor Grazing Act of 1939 and that, previously, a major route through the area linked regional trading posts. We also located camp sites with soldered cans, an ancient Marsh Pick head and hand wrought awls.

We knew that Charles H. Sternberg certainly collected in the general region of the Fossil Forest area (Sternberg, 1932), and based upon this record that places him very near the Fossil Forest and at trading posts around it, there is a reasonable likelihood that the grand old man of fossil hunting, and later possibly his son George, excavated in the Fossil Forest in the early 1920's. The dinosaurs and other fossils they collected in the Fossil Forest were most likely sold to various institutions. One must remember that during this period of time, the best maps available were rudimentary, most land was not fenced and settlements were few and far between.

Additional records were forthcoming that placed a later field party both very near and actually in the Fossil Forest. This was a party led by J. W. Stovall in the

1940-41 period. These records, include a photo that looks much like one of the trees and surrounding area in the Fossil Forest. A second group of quarries are probably associated with him, and specimens may be in the University of Oklahoma collections.

A third series of quarry sites exists and includes some major digging operations. These sites probably date from the mid-1970's. No institution seems to have documented collections available from these sites. Thus, we were late-comers to the Fossil Forest, possibly the fourth group to work in the area.

THE FIRST BABY DINOSAUR, NESTS, EGGSHELLS AND EGGS FROM NEW MEXICO

Digging for fossils is always an adventure; you never know what will turn up. We knew that during the Late Cretaceous, the Fossil Forest locality was situated very near sealevel and near the seashore. It seems likely that the area was periodically inundated, resulting in drowned forests and floated logs. We also had evidence of marine sharks, bivalves, gastropods and an ammonite. For many years we believed that the dinosaurs of the Fossil Forest nested inland or upland from coastal areas and never expected to find dinosaur eggs, eggshell fragments, or the skeletal remains of infants.

It happened of course; at a quarry site being excavated by Jim Baldwin, of Silver City, and Mary Ann Pattison, of Carrizzozo, an infant dinosaur lower jaw emerged just below an adult rib fragment. The quarry is located at the margin of a channel fill sandstone. Subsequent work in an extension of the quarry into the same channel located adult hadrosaur pelvic and limb bones. The infant jaw consists of most of the dentary with teeth and an edentulous predentary. The teeth are typically hadrosaurine and virtually pristine. The infant was very young, if not a very recent hatchling. It seems most likely that the infant is *Edmontosaurus* ("Kritosaurus"), or *Parasaurolophus* (Wolberg, 1992b). The quarry site is located between the fourth and fifth forest levels and, based upon palynological data (Jameossanaie and others, 1990), lies above the boundary between the Campanian-Maastrichtian Stages and must be about 72-73 million years old.

Elsewhere in the study area, almost due west and up-dip at about the same stratigraphic level, we discovered a site that yielded bone fragments, teeth, and eggshell fragments that have been identified as dinosaur shell material. It is very likely that we were within the same paleodrainage as at the jaw locality, and possibly even the same stream. Still further west, we located and excavated an area with resistant structures that we interpret to be empty dinosaur nests. These features are subcircular, buff colored, silty sandstone different from the surrounding matrix; they are concave and appear to be scooped out hollows with a great deal of now carbonized plant debris in several layers inside but near the top

of the features. The tops of the features must have been elevated above the surrounding ground level because material appears to have been kicked or scratched over the sides of the feature. One of the excavated features contained a large coprolite. As noted above, no eggs were found in any of these features. We did locate thin leaf accumulations between several of the structures and the structures themselves appear to be regularly spaced rather than randomly distributed.

Away from the Fossil Forest, very low in the Fruitland Formation, indeed at a stratigraphic level where the Fruitland and marine Pictured Cliffs Formation virtually intertongue with each other, we discovered, quite by chance, nests of intact and complete dinosaur eggs. This proved once again that in field paleontology one should expect the unexpected. We were busily collecting sediment and resin samples and completely by chance just about tripped over the first nest we found. The eggs are elliptical, approximately football-shaped, and are five to seven inches in length. The external surfaces of the shells are corrugated, rugose and otherwise crenulated in a more or less a regular pattern from egg to egg (Wolberg and Bellis, 1990; Wolberg, 1992b; 1992c). Many nests occur in the area, and it is of some interest that we identified in-place logs and isolated logs in the area; at least three levels of stumps were present. Based on a late Campanian date of about 74-75 million years for the top of the Pictured Cliffs Sandstone, this egg site low in the Fruitland, is older than the Fossil Forest localities and, conceptually at least, would fit nicely in the 73-72 million year range.

It appears reasonable to note some ideas about the dinosaur nesting environments that seem to apply to the Fruitland Formation. The fossil animal, botanical, and palynological data indicate that the Fossil Forest was situated at sealvel and was periodically inundated by the sea. In addition to a diversity of fishes, including at least periodic abundances of sharks, amphibians, lizards, turtles and crocodiles are present. The dinosaur fauna seems to be a typical Fruitland fauna; the mammals reported offer the best look at San Juan Basin mammals yet documented. Dinosaur nesting seems to have occurred on sandy flats near the termination of a broad meandering river system that at least locally emptied into a lagoon. Palm groves were present in the area and cypress bordered rivers and tributaries. Slightly better drained areas were populated by deciduous trees and redwoods. If I interpret the data correctly, it would seem that dinosaur nesting areas were associated with water because periodic inundation and drowning of nests is what led to preservation of the evidence. Nearness to water may or may not be the determining factor in dinosaur nesting areas.

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states. Our science teacher program was obviously a summer program, but it always struck me as being remarkable that teachers would give up their vacations to spend weeks in the San Juan Basin or in classrooms and laboratories in Socorro. Some of our teachers came back year after year and "made" us create new courses for them to take. It is very apparent, and our science teachers have told us, that recent interest in improving science education could find no better vehicle than field, laboratory and "lecture hall" paleontology to attract and maintain the interest of students. More than any other scientific endeavor, paleontology exposes students to a diversity of ideas and concepts that are truly interdisciplinary. I am also grateful to the many graduate students and scientists from many institutions and agencies that took part in our work in one way or another. Most especially I want to thank Frank Kottlowski, Director Emeritus of the New Mexico Bureau of Mines and Mineral Resources, for his interest and support of our work and for the interest in public responsibility that he felt a tax funded agency should maintain. Finally, I want to thank Gary Rosenberg for his review of the manuscript.

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Hunting Ancient Dragons in China and Canada

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INTRODUCTION

I was eleven years old when I read a book by Roy Chapman Andrews (1953) that changed my life. It was a book about dinosaurs, those magnificent animals that had captured my interest when I was even younger. But more significantly, the book was about looking for the remains of these ancient dragons in the Gobi Desert of China and Mongolia, and for the first time I learned that there was a potential career in hunting dinosaurs. The day I read the book was the day I decided to become a paleontologist. But in my wildest dreams I never imagined that I would follow in the footsteps of Andrews and end up in the Gobi Desert.

The Royal Tyrrell Museum of Palaeontology developed as a concept when I was at the Provincial Museum of Alberta in Edmonton, and was approved for development by the Government of Alberta at the end of 1980. Detailed planning for construction of the building, moving collections and staff, etc., was done in an office in downtown Edmonton. One of our employees, Brian Noble, decided not to move to Drumheller, and we said goodbye to him in mid-1982. But before we parted, he came to me and asked what I would like to do after the museum opened. It was a whimsical question, or so I thought. Without hesitation I told him I wanted to collect dinosaurs in the Gobi Desert. There was the appeal of going to an exotic place from which the excavation of dinosaurs had been so influential on the development of my career. But more importantly, there were sound scientific reasons for wanting to compare the dinosaurs of that region with those I had been collecting in Alberta since 1976.

It has long been known that families of dinosaurs from both the Lower Jurassic and the Upper Cretaceous have representatives in both Asia and North America. However, starting in Middle Jurassic times, there were natural barriers to faunal movements between the northern continents. Nobody is really sure when contacts were re-established, but there appears to have been some faunal interchange in Early Cretaceous times. Between 1930, when the American Museum of Natural History expeditions finished (Andrews 1932), and the mid-1980s, direct comparison of specimens from the two continents was difficult for political reasons. Furthermore, information from central Asia was scanty on the mode of occurrence of fossils, the association of fossil plants and animals, the

structure and composition of the rocks they are found in, and all of the other details that are required to interpret ancient climates, environments and ecosystems. Therefore, one could never be sure whether or not apparent faunal differences were environmentally controlled.

When Brian Noble left our employ, he looked for grants and other forms of support, and started talking to people about the feasibility of working in central Asia. Eventually he established the Ex Terra Foundation, a non-profit organization that was initially set up to promote and develop an expedition to collect dinosaurs in the Gobi Desert. One month after the Royal Tyrrell Museum of Palaeontology opened its doors in September, 1985, we signed an agreement with representatives of the Chinese government.

The expeditions of the Dinosaur Project (China-Canada-Alberta-Ex Terra) were better known as the Canada-China Dinosaur Project. They were operated by staff at the Canadian Museum of Nature (CMN) in Ottawa, the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing, and the Royal Tyrrell Museum of Palaeontology (RTMP) in Drumheller, who were to study and compare the dinosaur faunas and their paleoecology in central Asia and North America. This work was sponsored by the Chinese Academy of Sciences, the governments of Alberta and Canada, and the Ex Terra Foundation of Edmonton (who also took an active role in expedition logistics), and was supported by grants from the Donner Foundation (Toronto) and a number of private corporations. The scientific coordinators were Dong Zhiming (IVPP), Dale Russell (CMN) and Philip Currie (RTMP). Other Canadian and Chinese palaeontologists and geologists were brought on to create a multidisciplinary team that included specialists in palynology, invertebrates, turtles, lizards, crocodiles, birds, mammals, dinosaurs, dinosaur footprints and sedimentology. To meet project objectives, we decided to send expeditions to sites in northern China (Xinjjiang and Inner Mongolia), the Canadian Arctic islands (Axel Heiberg, Bylot and Ellesmere), and Alberta (Devil's Coulee, Dinosaur Park, Grande Cache, and Grande Prairie).

The expeditions started in 1986. A survey team visited a site in Xinjiang to assess its potential, and to work out some of the logistics problems. Staff of the IVPP and the Inner Mongolia Museum (Hohhot) came to Canada to join field crews in the Arctic on Axel Heiberg and Ellesmere Islands, and in Alberta. Although no dinosaur bones were discovered in the Arctic, many significant specimens were collected in Dinosaur Provincial Park, including a nicely preserved braincase of the small theropod *Troodon*. Near Grande Prairie (Alberta), the excavation of a bonebed dominated by the remains of the ceratopsian *Pachyrhinosaurus* was started with very promising results.

The first major expedition to China took place in the Junggar Basin of Zinjiang in 1987. At the end of the field season, some of the field crew drove across northern China to investigate potential sites for the 1988 expedition. Four

localities (Bayan Mandahu, Chabu Sumu, Erenhot and Tsagan Nor) were considered to be interesting and productive enough for further investigation, although time constraints restricted major work in future years to Bayan Mandahu and Erenhot. In Canada, the dinosaur egg site at Devil's Coulee was discovered, and fieldwork continued in both Dinosaur Provincial Park and Grande Prairie.

By 1988, the Canadian-Chinese team had been split up into smaller groups so that several sites in China could be worked at the same time. One camp was set up in Xinjiang to continue work on two quarries that had been started in 1987, and to find and collect new specimens. The main camp at Bayan Mandahu amassed a large collection of dinosaurs during the month of June, then moved to Erenhot (Iren Dabasu) in July. Both groups met in the Ordos Basin of Inner Mongolia early in August. Lower Cretaceous specimens proved to be both interesting and highly significant. The 1988 fieldwork in China finished in the Alashan Desert close to a site discovered and worked by the Sino-Soviet expeditions of 1959 and 1960. In Canada, the Canadian Museum of Nature investigated a dinosaur report on Bylot Island in the Arctic, and found enough dinosaur bones to justify another joint Chinese-Canadian expedition the following year. Work continued in Alberta in Devil's Coulee, Dinosaur Provincial Park and Grande Prairie.

The Canada-China Dinosaur Project started the 1989 field program in Xinjiang in May. When this phase was nearing completion, the violent crackdown in Tien-am-men Square in Beijing caused an international furor, and all further field work in China was canceled for the year. Work did continue in Alberta at the same three sites, and the joint expedition to Bylot and Ellesmere Islands in the Arctic was considered to be a success.

The last excavation in Xinjiang was finally completed in 1990, although there was still lots more that could have been collected. The largest field party gathered at Bayan Mandahu in June and early July, and collected many significant specimens and data, and finished mapping our sites. This group moved to Erenhot for the last part of July to excavate a tyrannosaurid skeleton found in 1988, and a major number of nests of dinosaur eggs. A second smaller field party examined sites in the Ordos Basin. In Canada, a major new Lower Cretaceous dinosaur footprint site at Grande Cache produced dinosaur trackways and bird tracks. There was no Chinese participation in any of the other Alberta field sites in 1990, although they joined us again in Dinosaur Provincial Park in 1991.

Work in the Jurassic of China

In 1987, more than forty Chinese and Canadians gathered under the banner of the Canada-China Dinosaur Project to collect dinosaurs in the Middle and Upper Jurassic rocks of the Junggar Basin in northwestern China (Xinjiang). The

site is known as Jiangjunmiao, after the ruins of a desert inn that is one of the few cultural landmarks in the area (Fig. 1). Our Chinese colleagues had worked there in 1984, when they recovered the skeletons of an undescribed large sauropod and a new species of theropod called *Monolophosaurus jiangi* (Zhao and Currie 1993) from the Wucaiwan Formation.

		Hutubihe Formation
Lower Cretaceous	**Tugulu Group**	Qingshuihe Form.
Upper Jurassic	Shuixigou Group	**Shishugou Formation**
$J_{2,3}$		**Wucaiwan Formation**
Middle Jurassic		Xishanyao Formation
$J_{1,2}$		Sangongke Formation
Lower Jurassic		Badaowan Formation

Figure 1. Stratigraphy of Jurassic and Cretaceous rocks near Jiangjunmiao in Xinjiang, China. The Sino-Canadian expeditions worked mostly in the Shishugou and Wucaiwan Formations, and the lower part of the Tugulu Group.

The Sino-Canadian team excavated several enormous specimens from the Jurassic Wucaiwan and Shishugou Formations of Xinjiang, including the front end of a sauropod (*Mamenchisaurus sinocanadorum*) with cervical (neck) vertebrae up to 1.5 metres (5 feet) long, and cervical ribs as much as 4.1 metres (13 feet) in length. Although the body and tail were not recovered, comparison with *Mamenchisaurus* specimens from southern China suggest the total length of the animal would have been 26 metres (85 feet), which is the largest dinosaur presently known from Asia. The rock, unfortunately, was very hard and it took four field seasons to complete the excavation. Its skull was finally recovered in 1990, and conclusively showed that mamenchisaurids are not closely related to the diplodocids (i.e., *Diplodocus*, *Apatosaurus*) of North America.

A nearly complete skeleton of a well preserved, new species of large theropod was found close to the sauropod skeleton (Fig. 2). Distantly related to *Allosaurus*, *Sinraptor dongi* was a mere seven metre (23 foot) long carnivore closely related to *Yangchuanosaurus* from southern China.
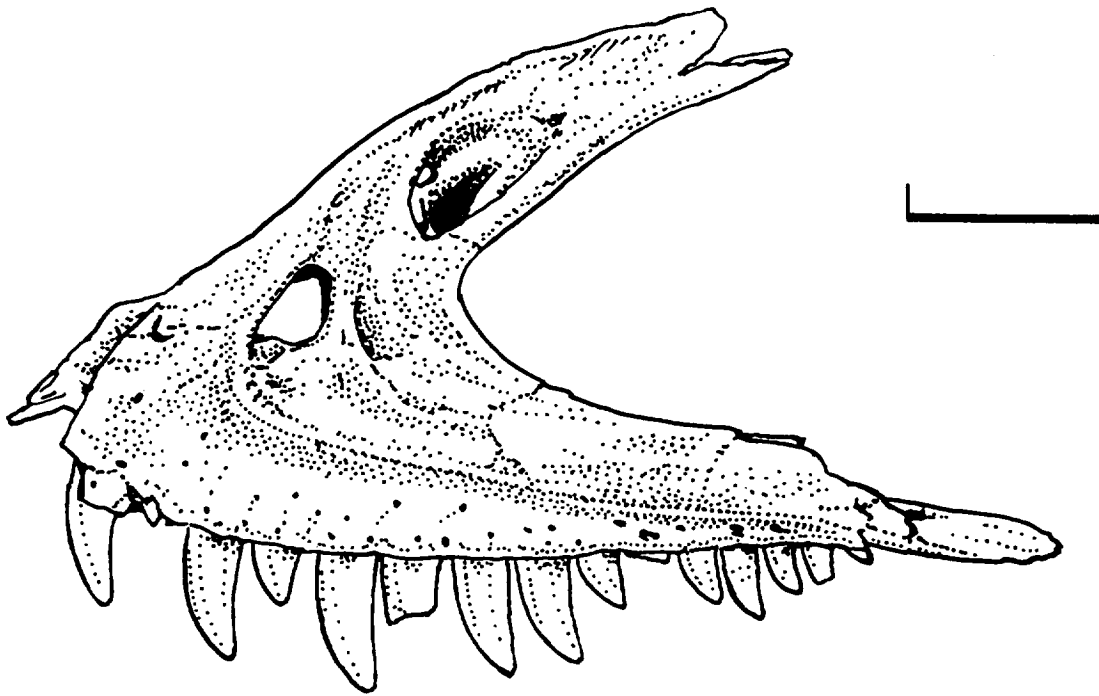
Figure 2. Left maxilla of *Sinraptor dongi*. Scale = 10 cm

The Middle and Upper Jurassic rocks of Xinjiang proved to be very rich, although the hardness of the rock prevented us from removing more than a few of the many dinosaur skeletons that were discovered. Several "fossil forests" were found during the course of the work in Xinjiang, along with numerous specimens of turtles, crocodiles and small herbivorous dinosaurs.

Lower Cretaceous

A great deal of effort was expended at Lower Cretaceous localities in China and Canada to determine when intercontinental faunal exchanges were initiated. The Tugulu Group in Xinjiang produced the abundant remains of pterosaurs, turtles, crocodiles, and small dinosaurs characteristic of the Asian *Psittacosaurus*-pterosaur fauna. In Inner Mongolia, the Ordos Basin has strata of similar age. Here field parties collected many specimens of *Psittacosaurus*, complete champsosaur (*Ikechosaurus sunailinae*) skeletons, and a new species of stegosaur (*Wuerhosaurus ordosi*). One of the new species of turtles recognized in the expedition collections was *Sinemys gamera*, an unusual form with wing-like processes extending from the shell.

The most remarkable find of all the expeditions of the Dinosaur Project was an almost complete skeleton of a small theropod from the Ordos Basin. This

turkey-sized animal was curled up as though it had died in its sleep. In 1856, *Troodon formosus* became one of the first dinosaurs described from North America. Recently it has been shown that troodontids were large-brained dinosaurs closely related to the origin of birds. *Sinornithoides youngi* is the most complete troodontid specimen ever found in Asia or North America, and revealed anatomical characters that were previously unknown for this important family of dinosaurs.

In 1988, a Dinosaur Project party worked in the Alashan Desert of Inner Mongolia in the Lower Cretaceous Bayan Gobi Formation. Vertebrates recovered included psittacosaurs, sauropods and champsosaurs. One of the more unusual finds was a new type of therizinosauroid (segnosaurian) dinosaur called *Alxasaurus elesitaiensis*. These unusual dinosaurs were unknown until recently, and their systematic position was unresolved until the Chinese material established that they were theropods.

Lower Cretaceous dinosaur footprint sites were visited in the Ordos Basin in 1987 and 1990, and in Alberta in 1990 and 1991. The footprint locality near Grande Cache (Alberta) is close in age to the Ordos Basin sites in China, and the footprints are similar in morphology. Unusual theropod tracks (*Buckeburgichnus*) that always have four toe impressions rather than three have been recovered from these widely separated localities. Unfortunately, footprints of similar shape can be made by animals that are not closely related, and therefore the similarity of footprint types only hints at faunal interchange.

In 1986, the Canada-China Dinosaur Project expedition to Axel Heiberg Island failed to find Arctic dinosaurs in the Lower Cretaceous Isachsen Formation. Other types of fossils were collected, however, and helped define the depositional environment of this formation.

Late Cretaceous

Iren Dabasu was the site where Roy Chapman Andrews and other staff of the American Museum of Natural History collected the first central Asian dinosaurs in 1922. Located near the present day border city of Erenhot, little has changed near the place where they camped more than seven decades ago, and the quarries of the expeditions that preceded us were located with relative ease. Because of similarities in the ancient environments, the dinosaur fauna of the Iren Dabasu Formation is closer in some ways to North American dinosaur faunas than to those of other central Asian sites. Both flat-headed hadrosaurid (*Gilmoreosaurus*) and crested lambeosaurid (*Bactrosaurus*) hadrosaurs were found, along with a surprising abundance of the primitive ornithomimid *Archaeornithomimus* . Two species of large carnivores and several small theropods were represented by isolated bones and teeth. A skeleton of the tyrannosaurid

Alectrosaurus was collected in 1990. A dromaeosaurid (closely related to *Velociraptor*), a troodontid (similar to *Saurornithoides*) and the birdlike *Avimimus* were identified on the basis of isolated teeth and bones. A significant difference from North American sites is the presence of two or three genera of therizosauroid theropods. Sauropod bones were also found in the bonebeds dominated by hadrosaurs. Six distinct types of eggs and/or eggshell were identified. Several nests of dinosaur eggs were collected, including some from what appears to have been a nesting site with at least five nests (each with a dozen eggs) (Fig. 3).
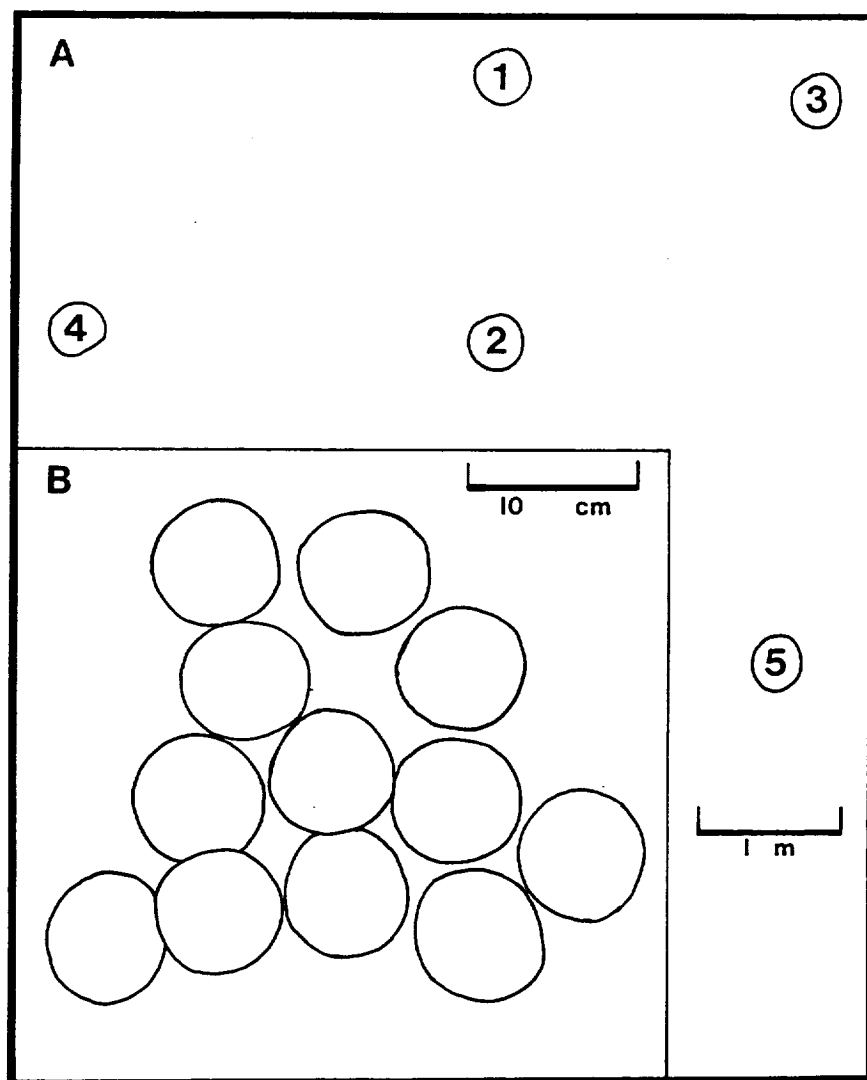
Figure 3. A) Layout of 5 nests of eggs found in the Iren Dabasu Formation at Erenhot, China. Nests 1, 2, 3 were excavated and are in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing. Additional nests were present, but were largely destroyed by erosion. B) Map of eggs in IVPP 250790-3, Nest 3.

Most of the collaborative work in Alberta was done in Dinosaur Provincial Park. One of the most significant specimens collected was a braincase of *Troodon* that was described in 1993. Because the semicircular canals, and the air ducts and sinuses associated with middle ear, are well-preserved, it provides information on the transition between dinosaurs and birds. The braincase had been found in 1986 by Tang Zhilu, who distinguished himself by finding a nice *Edmontonia* skull when he returned to the Park in 1991. A bonebed near Grande Prairie, Alberta, produced thousands of specimens, and appears to have been a mass death site. Juveniles and two adult morphs (presumably male and female) have been identified for this new and rather bizarre species of *Pachyrhinosaurus*. Several nests of eggs with embryos have already been collected from Devil's Coulee in southern Alberta, and a new species of the crested hadrosaur *Hypacrosaurus* is being described by Horner and Currie (in press).

Upper Cretaceous beds on Ellesmere Island failed to produce dinosaurs in 1986. The Sino-Canadian Arctic expedition of 1989 collected dinosaur and bird bones from Bylot Island, and possible fragments of dinosaur bones from Ellesmere Island.

The 1988 and 1990 expeditions to China were conducted mostly at Bayan Mandahu, where there are extensive Upper Cretaceous exposures equivalent to the Djadokhta Formation of Mongolia. Protoceratopsians (apparently including *Bagaceratops*, *Protoceratops*, and *Udanoceratops*) are the most commonly recovered dinosaurs, and ranged in size from a two centimeter long embryonic skull to an adult with a skull one meter in length. A group of five parallel protoceratopsian skeletons were found on the side of a "fossilized" dune, and were apparently buried in a sandstorm some 75 million years ago.

Another locality produced twelve *Pinacosaurus* juveniles, each of which were 1.5 m (5 feet) long. Two areas were excavated at the site, separated by 20 meters (66 feet). The first yielded five individuals that were grouped randomly together, although the presence of *Velociraptor* teeth suggests that their gravesite had been disturbed. The other section had seven more individuals that were lying more or less parallel to each other. Their alignment and the composition of the surrounding sediments suggest that they probably died of suffocation when they were buried by shifting sands in a wind storm. Like the *Protoceratops* site, the evidence suggests that *Pinacosaurus* was a gregarious dinosaur. The baby ankylosaurs have some armor on the skull and two bands of armor plates on the neck. The rest of the body was covered by little nodules of bone, but each had a diameter of less than a few millimeters and was obviously just the beginning of a bony plate. So for all intents and purposes the body of a baby ankylosaur was unprotected, and there is no sign of a tail club.

Hundreds of specimens were collected at Bayan Mandahu, and the work of preparing and describing them is still in its early stages. A long legged *Saurornithoides* baby shows how birdlike troodontids looked. *Oviraptor* ("egg thief") received its name because the first skeleton found in Mongolia in 1923 was associated with what were assumed to be *Protoceratops* eggs. The Sino-Canadian expedition in 1990 found a partial skeleton of this theropod associated with a nest of eggs. This time, however, the animal was sitting on top of the nest, suggesting that it may have been incubating and protecting its own eggs. Lizard skulls and skeletons are relatively common at Bayan Mandahu, and specimens found by the Chinese and Canadian team have extended the fossil record of amphisbaenids by 25 million years (Wu et al. 1993).

Direct comparisons could be made between the sedimentary features of the ancient desert represented in the rocks and those of the modern Gobi Desert at Bayan Mandahu. The low diversity of dinosaur species, in spite of a high recovery rate of specimens, is another indication that the rocks at Bayan Mandahu represent a dry paleoenvironment. The type of trace fossils left by insect larvae and other invertebrates are also suggestive of semi-arid to arid climatic conditions. And finally the entrapment of groups of protoceratopsians and ankylosaurs in catastrophic accumulations of sand could only have happened in regions with little vegetation cover. The differences seen in the faunas of this ancient desert in central Asia and the coastal lowlands of the Cretaceous of Alberta are therefore easily understood.

The expeditions of the Dinosaur Project (China-Canada-Alberta-Ex Terra) were large multidisciplinary, multinational teams that were extremely successful in collecting specimens and data. More than 60 tons of specimens are estimated to have been collected in China alone. Preparation of specimens and collaborative research will continue for a long time. The first volume of scientific results has been published (Currie 1993), and other collections of papers will appear in future years. Films and a popular book (Grady 1993) are also available. A traveling exhibition has been assembled using mostly new species of dinosaurs that were collected by the Sino-Canadian expeditions. "The Greatest Show Un-Earthed" was seen by hundreds of thousands of visitors in Edmonton and Toronto in 1993, and starts its Japanese tour in 1994.

ACKNOWLEDGEMENTS

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The Enigmatic Dinosaur Faunas of Australia

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ABSTRACT- Australia has a scant but significant record of dinosaurs which includes a prosauropod, two or three sauropods, at least four theropods (including carnosaurs and an ornithomimosaur), four hypsilophodontids, an aberrant iguanodont, a primitive thyreophoran (possibly an ankylosaur), and a possible primitive neoceratopsian. Footprint fossils indicate higher taxonomic diversity, including small bipedal ornithopods and coelurosaurs, very large sauropods, large carnosaurs, and a stegosaur. The most diverse dinosaur assemblage, from the Early Cretaceous of Victoria, represents a polar dinosaur community that lived within the Cretaceous Antarctic Circle.

INTRODUCTION

When thinking of dinosaurs, images of *Tyrannosaurus, Triceratops, Apatosaurus* and *Stegosaurus* spring to mind. All of these come from North America. Indeed, we usually always regard dinosaurs as creatures that have been dug up from other countries except Australia. The land downunder does have its own dinosaurs although most are known from only a few scrappy bones with the exception of two cases known from nearly complete skeletons (Fig. 1). Yet despite this, Australia's dinosaurs are actually very interesting from a number of scientific angles - they represent a dinosaur fauna that was antipodean compared to the well-known dinosaur faunas from North America and Asia; some lived within the ancient Antarctic Circle, surviving long annual periods of cold and darkness, and some are biogeographically enigmatic. Most importantly, we are finding more dinosaurs from Australia each year. Australia is in the middle of a palaeontological gold rush - about half its known species of dinosaurs have been discovered in the last decade or so.

Although few really large dinosaurs have been found in Australia many recent finds of small dinosaurs, and their footprints, are filling in big gaps in the history of dinosaurs from the southern continents. At the beginning of the age of dinosaurs, in the Triassic Period (about 230 million years ago), Australia formed the eastern extremity of Gondwana, the great southern supercontinent. Gondwana was formed by Antarctica, Australia, New Zealand, India, Arabia, South America and South Africa. During the Triassic it lay in close proximity to the northern supercontinent of Laurasia, containing Europe, Asia and North America.

The first dinosaurs appeared about this time in South America. Land bridges then permitted dinosaurs to migrate into all the continental land masses. By the early part of the Jurassic Period (about 200 million years ago) as much of Gondwana began to rift apart - South America and Africa had left Gondwana - most of the major dinosaur groups had evolved. By the Early Cretaceous (about 100 million years ago) dinosaurs reached their peak of diversity. Only Australia and Antarctica still remained joined to form the last remnant of Gondwana. Australia's dinosaur faunas had now become established after a long period of evolution in isolation. Dinosaur groups that appeared

late in the Cretaceous in the northern hemisphere, such as the duck-billed hadrosaurs, couldn't migrate into Australia because the continents were then separated by the newly formed oceans.

Dinosaurs undoubtedly reached Australia through Gondwana sometime between the late Triassic and early Jurassic. Evidence for this migration has been recently discovered in Antarctica - the remains of a large carnivorous dinosaur was discovered on the top of Mt. Kirkpatrick near the Beardsmore Glacier in the 1990/91 season by British geologist David Elliot, and excavated by Bill Hammer of Augustana College, Illinois. Helicopters had to air-lift the heavy slabs of plaster-jacketed rock containing the bones down from the mountain top, back to McMurdo Base. The specimen turned out to be a carnivorous dinosaur with a pair of raised bony ridges on top of the skull. These, and other recent dinosaur finds from Antarctica, testify to its use as a migratory pathway for dinosaurs to invade Australia.
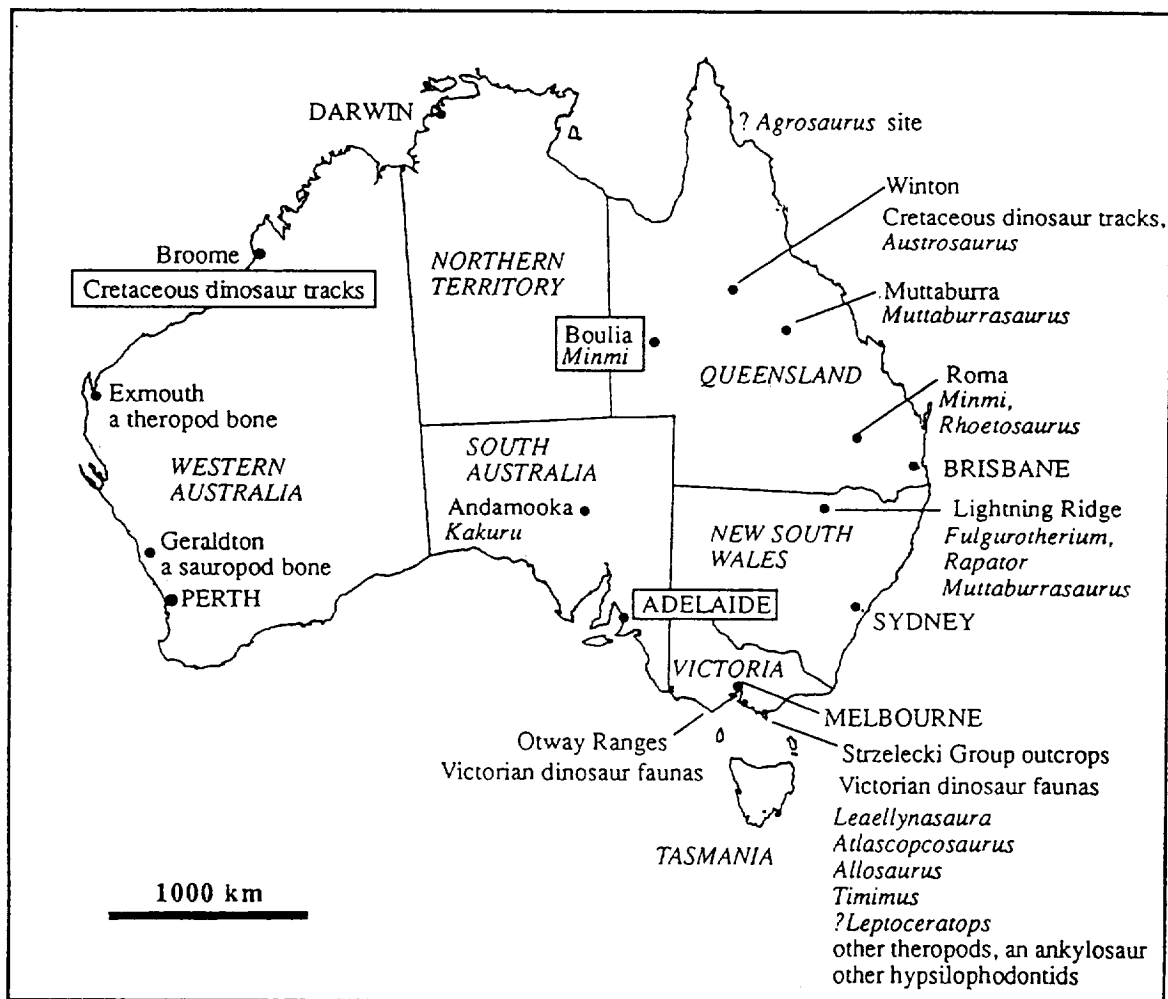
FIGURE 1. Map showing locations of dinosaur finds in Australia.

Australia's oldest known dinosaur is of probable Late Triassic or earliest Jurassic age. *Agrosaurus macgillvrayi* was found by the exploration party of HMS Fly in 1844 off the coast of northern Queensland, and described by Seeley (1891). Later Galton and Cluver (1986) identified it as a prosauropod with affinities to *Anchisaurus*. In recent years the type specimen, consisting of two tibiae, and a claw, was prepared by the Natural History Museum (London) and some extra bones came out of the matrix, including a vertebra. Currently workers in northern Queensland are trying to relocate the site which was not clearly labelled with the specimens.

EARLY FINDS: DINOSAURS OF THE DEPRESSION

Australia has an interesting history of dinosaur discoveries. Some of our larger specimens were uncovered in Queensland during the depression of the late 1920s. The Queensland Museum did not have funds to send out scientists into the field so the large bones had to be "packaged up and sent in" by the farmers. This is how *Rhoetosaurus*, was found (Longman, 1926,1927). *Rhoetosaurus* was named after the mythical Greek giants, the Rhoetos. It was a long-necked sauropod estimated to be 15 metres long and weighing up to 20 tonnes, but, as we lack the full extent of the neck (in fact there is only one cervical vertebra; Fig. 2), its exact size and shape cannot be determined. It is believed to be a relatively unspecialised cetiosaur. It is known from a partially complete skeleton, consisting of several limb bones, vertebrae, and bones of the hip and shoulder. Heber Longman, then Curator at the Queensland Museum, described and named these bones but never actually visited the site near Roma. This lead Dr. Mary Wade and Dr. Tony Thulborn to go back to the *Rhoetosaurus* site, on Taloona Station, in the mid 1970s. 70 years after *Rhoetosaurus*' discovery they uncovered a nearly complete foot of the same animal as well as several other pieces of bone (Thulborn, 1985).

Longman also named another sauropod, *Austrosaurus* (meaning 'southern lizard'), from some isolated backbones sent in from Clutha Station, near Maxwelton, in northern Queensland (Longman, 1933). More material thought to belong to *Austrosaurus* was found in 1959 on Alni Station by Dr. Alan Bartholomai of the Queensland Museum. These bones comprised more vertebrae, and also hip, leg, and hand bones (Coombs and Molnar, 1981). The simple tail vertebrae lack struts and buttresses and lack hollow cavities that are found in more advanced sauropod families. The bones suggests that the arms were relatively long and slender, like older Jurassic sauropods from North American localities. It seems likely that *Austrosaurus* was a late survivor of a primitive sauropod family, the Cetiosauridae. It was of similar size to *Rhoetosaurus*.
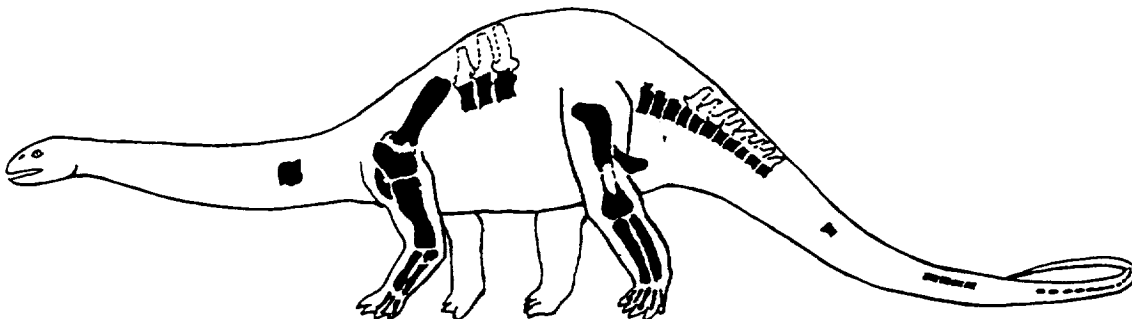

FIGURE 2. *Rhoetosaurus brownei*, from the Middle Jurassic of Queensland, is Australia's best known sauropod dinosaur. This diagram shows how much of the skeleton is known.

Australia's largest dinosaur is known from one fragmentary neck bone found near Hughenden, Queensland. The bone closely resembles that of the well-known gigantic African and American genus *Brachiosaurus*, and suggests that the Australian species was up to 22 metres long (Molnar, 1991). However, as the neck vertebrae of *Austrosaurus* are not yet known, this find could possibly come from *Austrosaurus* rather than a brachiosaur.

SKELETONS OF FIRE: OPALISED DINOSAURS

The opal mining frenzy of the early 20th century uncovered more Australian dinosaurs. The British Museum (Natural History) obtained a small collection of Australian dinosaur bones, preserved as bone pseudomorphed by opal during the late 1920s, and these were studied by a German dinosaur expert, Fredrich Von Huene. His study (Von Huene, 1932) recognised a leg bone from a small plant-eating hypsilophodontid dinosaur, and a hand-bone and tail vertebra from carnivorous theropods. All these specimens came from the Lightning Ridge opal fields in northern New South Wales, from Early Cretaceous sandstones. Von Huene recognised three new Australian dinosaurs, two of which remain as valid species *(Fulgurotherium, Rapator)*, and one *(Walgettosuchus)* is doubtful, as it is based on a single rather featureless tail bone.

Fulgurotherium australe takes its name from the Greek meaning " southern Lightning beast", alluding to the Lightning Ridge locality, and was described from an isolated thigh bone by Von Huene. It has also been recently found from the coastal exposures of Victoria. It was small plant-eating hypsilophodont dinosaur of about 1-2 metres in total length. So far only thigh bones have been identified although a number of isolated hypsilophodontid bones and teeth occur in the same deposits that are most probably part of the same animal. *Fulgurotherium* was reviewed by Molnar and Galton (1986).

Rapator ornitholestoides was named by Von Huene (1932) from a single fossilised hand bone (metacarpal, Fig. 3) which resembled that of the North American dinosaur *Ornitholestes* in having a well-developed posterolateral process. The name *Rapator* (meaning "predator") reflects the fact that it belonged to a theropod. Despite only having the one bone it has stood the test of closer examination and today remains as a valid genus, possibly allied to the abelisaurids of South America (Molnar, 1991). *Rapator* was probably a large animal of 8 or 9 metres length.
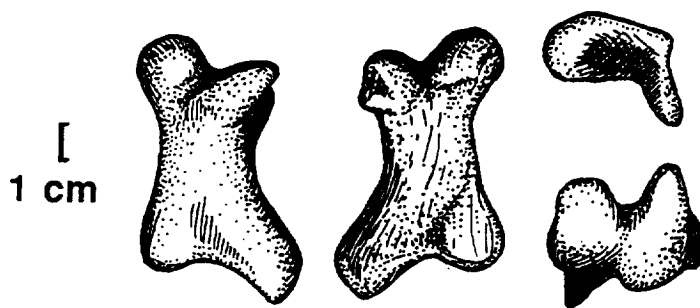

FIGURE 3. Metacarpal bone of *Rapator ornitholestoides*, Early Cretaceous of New South Wales (pseudomorph in opal).

Not all Australian dinosaur specimens remain in Australia. In the late 1970s a broken leg bone and claw of a dinosaur was found near Andamooka, in South Australia, preserved as a replacement by precious opal. This remains the only known record of

dinosaurs from that state. The bones were described and named as a new type of slender theropod dinosaur by Ralph Molnar and Neville Pledge in 1980. The name *Kakuru kujani* is from the aboriginal myth of the rainbow serpent and the name of the local tribe, the Kujani. The original bones, being of valuable opal, were sold at an auction and have since been lost to science. Fortunately an accurate cast of the specimen was made and is now held in the South Australian Museum. *Kakuru* was a slender bird-like dinosaur, probably about 3 metres long, whose tibia is of similar proportions as that of a heron or a crane, and resembles the strange bird-like dinosaur *Avimimus* from Mongolia.

MORE RECENT FINDS OF QUEENSLAND DINOSAURS

Australia has one dinosaur that sticks in everyone's memory. It is *Minmi paravertebra* a small armoured dinosaur with a delightfully short name, taken from its discovery site near Minmi Crossing, close to Roma, in southern Queensland (Fig. 1). The first specimen was found in 1964 and shows a series of backbones, part of the foot, and several thousand small, round, bony platelets that sat in the skin and protected the belly (Molnar 1980). The vertebrae of *Minmi* have unusual struts linking the processes on the backbones and may have supported the back to bear the weight of the belly armour, as the armour on the back was much reduced (Fig. 4). It may have tried outrunning its attackers rather than relying on heavy back armour for protection, like many other dinosaurs of its family. It is thought to have lived on a large island as eastern Queensland was then separated by shallow seas on all sides.

A nearly complete *Minmi* skeleton was found in early 1990 near Boulia, north-western Queensland (illustrated in colour in Long, 1993b). The back has a cover of well-spaced, rounded bony plates making the armour appear quite thin. The new specimen has a well-preserved head, most of the body and hip, and some of the limb bones. Both of the *Minmi* specimens appear to represent dessicated carcasses of dinosaurs that drifted out to sea before falling into the limey marine sediments. *Minmi's* relationships are enigmatic. It shares some ankylosaur features, (e.g. snout arches higher then the skull) yet retaining many primitive features expected to be found in an
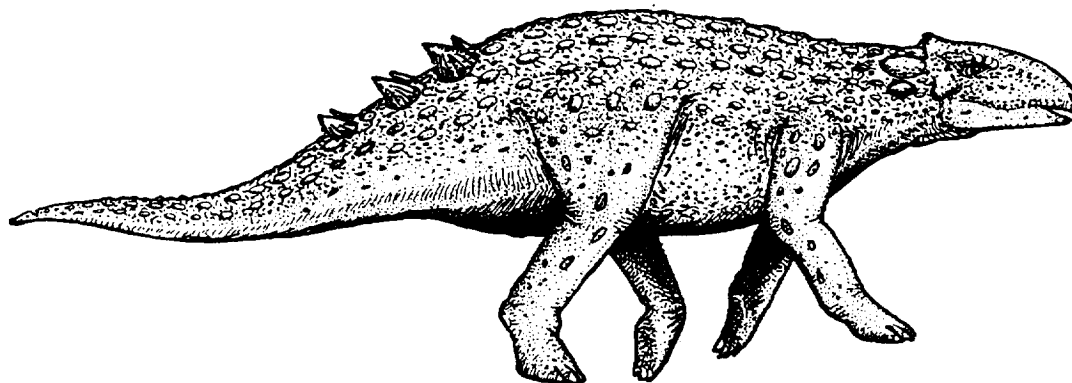

FIGURE 4. Possible reconstruction of *Minmi paravertebra*, from the Early Cretaceous of Queensland.

ancestral thyreophoran, the group containing stegosaurs, nodosaurs and ankylosaurs (e.g. femur rounded in section; skull longer than wide; acetabular and postacetabular regions of ilium both long; Molnar 1994). Molnar suggests that in essence it is probably an

ankylosaur but as most of the known members of that group come from the last 10 million years of the Cretaceous in Asia and North America, an early form from Gondwana would be noticeably different, perhaps even representing an entirely new group of armoured dinosaurs.

Australia's most complete dinosaur skeleton was discovered in 1963. Large bones were found in a cattle yard on the Thompson River, near Muttaburra, central Queensland by a grazier, Mr. D. Langdon. He contacted the Queensland Museum who sent out Dr. Alan Bartholomai, who immediately recognised that much of a complete skeleton of a plant-eating ornithopod dinosaur was present. After excavating many of the bones Bartholomai discovered that many pieces that should have been preserved were curiously not there. Where had they gone? Further enquiries revealed that many of the local farmers had taken bones as "souvenirs". The Queensland Museum then issued a public plea and within three years most of the missing bones had been returned. The job of preparing the skeleton took several years, and the missing parts were then reconstructed (Fig. 5), using the shapes of bones from a closely related form, *Iguanodon*. This dinosaur, named *Muttaburrasaurus langdoni* (Bartholomai & Molnar 1981) was approximately 10 metres in length from snout to tip of tail. As in other iguanodontids *Muttaburrasaurus* possessed a thumb spike, but it was broader and flatter than in *Iguanodon*. Such sharp spikes may have been used defensively by jabbing attackers in the throat.

The skull of *Muttaburrasaurus* bears a remarkable high crest over the snout that may have supported a fleshy organ for making sounds, somewhat similar to that of *Iguanodon orientalis* from Mongolia. A second, more complete skull of *Muttaburrasaurus* was discovered in 1984 and is still being prepared at the Queensland Museum. Other remains
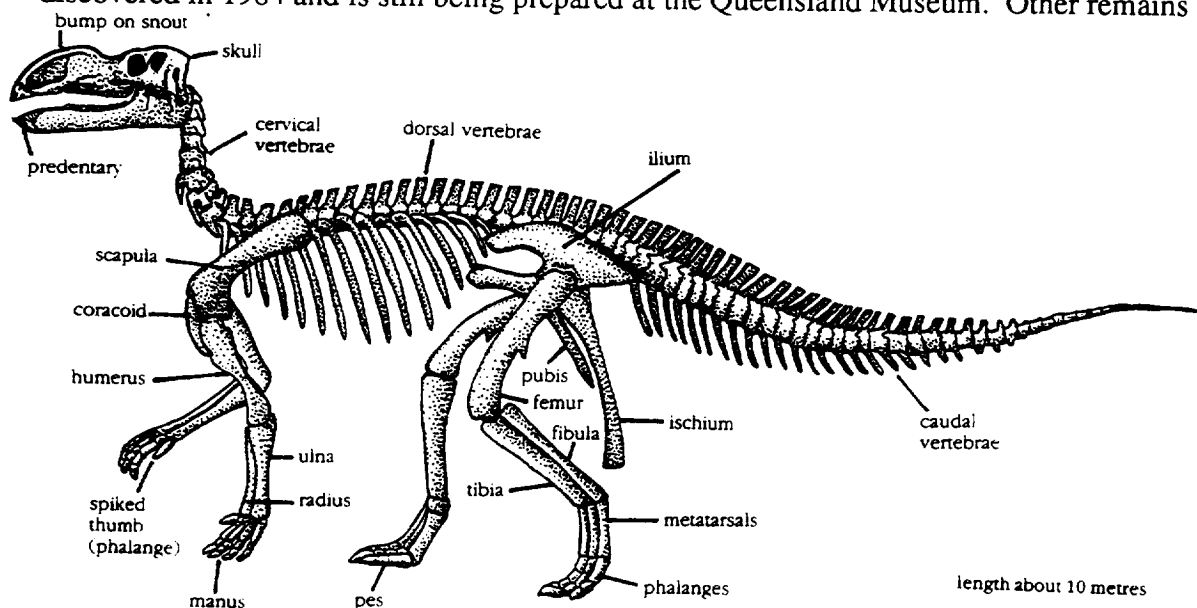
FIGURE 5: Reconstructed skeleton of *Muttaburrasaurus langdoni*.

of *Muttaburrasaurus* have been found near Hughenden, northern Queensland, and isolated bones from Lightning Ridge, New South Wales. The teeth and jaw structure of *Muttaburrasaurus* are unusual in that the tooth crowns are all erupted to the same degree, as if all the teeth erupted together. This differs from the normal condition seen in closely related dinosaurs in which teeth erupt in a spasmodic fashion. The jaws could

shear food rather than grind food, and there were large jaw muscle attachment areas giving great strength to the animal's chewing ability. *Muttaburrasaurus* may have even been taken to occasionally eating meat according to Bartholomai and Molnar (1981).

AUSTRALIAN DINOSAUR FOOTPRINTS - FILLING IN THE GAPS

While all these discoveries were being made in the eastern side of Australia, there was no record of dinosaurs from Western Australia until the 1950s. Dinosaur footprints belonging to a three-toed animal were discovered in the red sandstone near Broome and noted by Western Australian Museum Director Ludwig Glauert in 1952. In the 1960s an American palaeontologist, Edwin Colbert, accompanied Western Australian Museum expert Duncan Merrilees to Broome and they studied and made casts of the dinosaur trackways. Colbert and Merrilees (1967) named the footprints *Megalosauropus broomensis* meaning "the megalosaur-like feet from Broome". These footprints (Fig. 6)were up to 37 cm long, and belonged to a meat-eating theropod about 5-6 metres long. Many of the local people living in Broome have never seen the dinosaur foot prints because they are only exposed at very low tides.

In the mid 1980s a local naturalist, Mr. Paul Foulkes, often walked along the beach rocks exposed at Broome during very low tides and discovered many new types of dinosaur footprints. I have since examined the new discoveries with Dr. Tony Thulborn from the University of Queensland, and we believe that at least 6 different kinds of dinosaur species once inhabited the land around Broome. These include: two forms of gigantic sauropods (the largest footprints are just over 1 metre wide); large carnosaurs like *Megalosauropus* with footprints up to 53 cm long, indicating lengths of around 9 metres; small ornithopod dinosaurs, including *Wintonopus,* (Thulborn and Wade, 1984; Long, 1992a; Fig. 6) and a possible stegosaur -the first such record of this family of
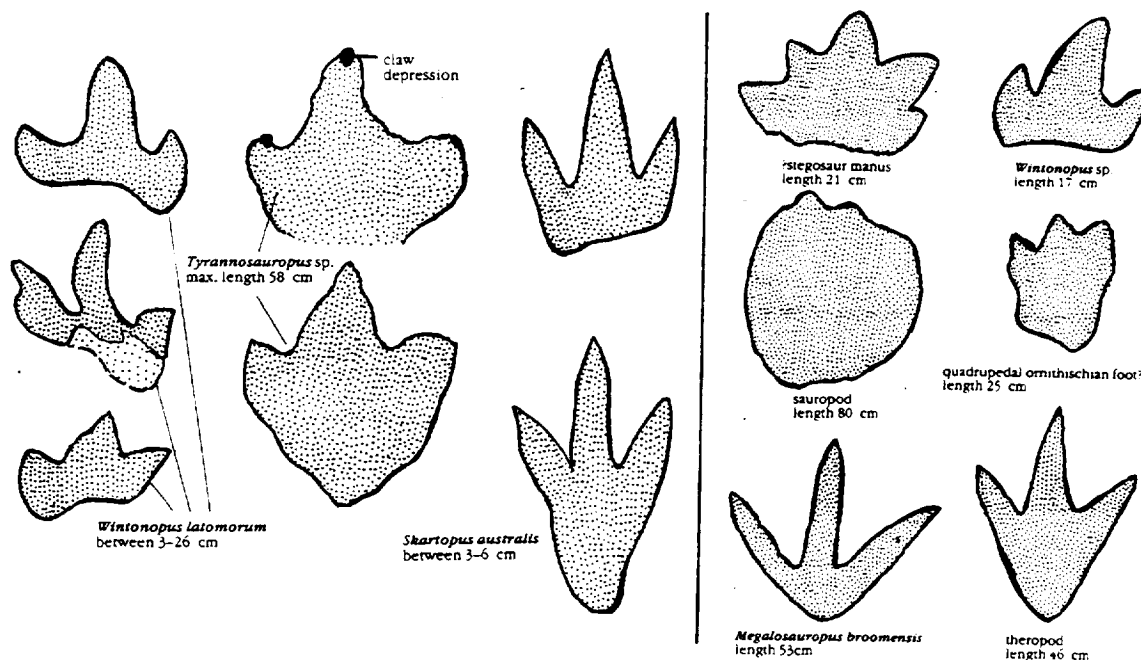
FIGURE 6. Dinosaur footprints from the middle Cretaceous Winton Formation, Queensland (left), and the Early Cretaceous Broome Sandstone, Western Australia (right).

dinosaurs in Australia. The stegosaur trackway is quite distinctive, being characterised by a stubby, asymmetric five-fingered handprint (Fig. 6) associated with a robust three-toed footprint (figured in Long, 1991). Such a combination is unique amongst dinosaurs, and is only found in advanced stegosaurs (Thulborn, 1990). The only skeletal remains of dinosaurs found so far in Western Australia are a possible theropod humerus (Late Cretaceous Mira Formation), a sauropod caudal vertebra (Middle Jurassic Colalura Sandstone; Long 1992b), and a recently found pedal digit from a theropod (Late Cretaceous Molecap Greensand).

Australia's most famous dinosaur trackways occur in Queensland. In the early 1980's a spectacular find of many thousands of dinosaur trackways was discovered near Winton. Careful excavation of the trackway bed was undertaken by Drs. Tony Thulborn and Mary Wade. The site contains nearly 3,300 individual prints belonging to three kinds of dinosaurs (Fig. 6). One was a small to moderate-sized ornithopod with a stubby asymmetric three-toed footprint, named *Wintonopus latomorum*.. The other was a small predator, probably a coelurosaur, whose sharp three-toed tracks have been named *Skartopus australis*. The third is a large three-toed carnosaur of gigantic size, leaving footprints up to 58 cm in length, and aptly named *Tyrannosauropus* (meaning foot like *Tyrannosaurus*).

The Winton trackways give us a fascinating glimpse of history -10 seconds of time about 100 million years ago. It appears that the two herds of small coelurosaur and ornithopod dinosaurs were coexisting harmoniously. The ornithopods may have been feeding on plants and the coelurosaurs could have caught the small insects and animals that fled from the disturbed vegetation. Suddenly the two dinosaur herds were disturbed by the giant predator. In desperation they tried to escape but were cornered in a closed valley and had no other means of getting away except to run past the big predator. The tracks show the carnosaur going one way whilst the little dinosaurs were stampeding around the predator, running as fast as their legs could carry them.

Thulborn and Wade's study estimates the speeds of the dinosaurs as up to 20 km/h for the swift ornithopods, 12 km/h for the coelurosaurs and 7 km/h for the big carnosaur. The trackways were so well-preserved because of the high clay content in the fine sandstone which probably baked hard in the sun, not long after the event, and was then later buried by wind-blown sands. Today there is a fine tourist display set-up at the site, called "Lark Quarry", and visitors can walk on a wooden ramp and view the thousands of exposed dinosaur footprints.

Other dinosaur footprints recorded from Australia come from the late Triassic and Jurassic of Queensland. The Triassic prints are of a large theropod with feet up to 46 cm in length similar to Eubrontes tracks from North America (Bartholomai 1966). Theropod tracks also predominate in the Jurassic of Queensland, including one unique ichnotaxon species, *Changpeipus bartholomai* (Haubold, 1971). An unusual small quadrupedal footprint has also been reported from Balgowan colliery, possibly an early thyreophoran (Molnar, 1991).

POLAR DINOSAURS FROM VICTORIA

The first dinosaur bone discovered in Victoria was a small claw from a carnivorous dinosaur found at Cape Patterson, near Inverloch, at the turn of the century (Woodward, 1906). It was not until the late 1970s that this site would once again start to yield dinosaur bones. In November 1978 Tim Flannery, Rob Glenie and myself found more bones and continued fieldwork by Tim Flannery with Tom Rich and Pat Rich lead to the discovery of many new sites along the coastal exposures in east Gippsland and in the

Otway Range in western Victoria, including the discovery in 1983 of "Dinosaur Cove", a rich site that has so far yielded many dinosaur bones and is still being excavated each year (Vickers-Rich and Rich, 1991). Most of the dinosaur bones belong to small hypsilophodonts - agile dinosaurs that ate plants and had no specialised features for defending themselves apart from their ability to run fast. In this way they resemble the deer or gazelles of the mammalian world today. The Victorian deposits have so far yielded the bones of at least four different types of hypsilophodont, three of which have been named and at least one other type that is still being studied.
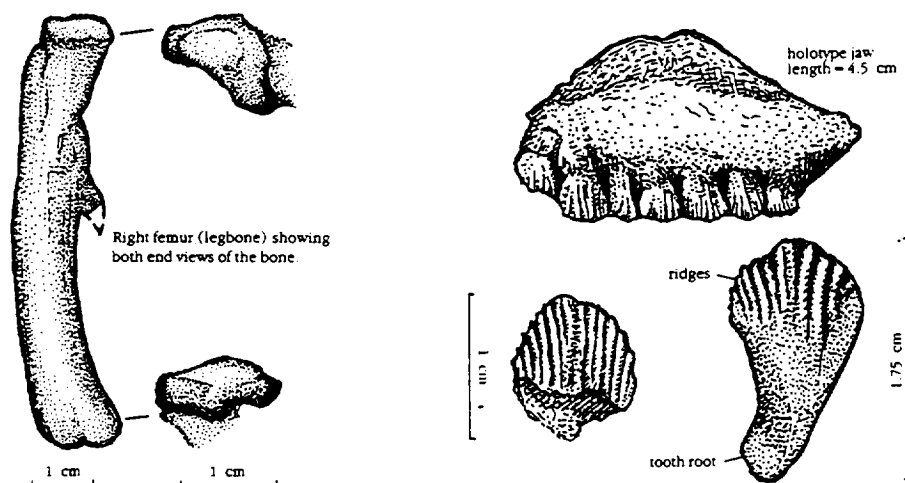
FIGURE 7. Victorian hypsilophodontids. Right femur of *Leaellynasaura amicagraphica* (left). Upper jaw (maxilla) and close-up of teeth of *Atlascopcosaurus loadsi* (right).

All of these were relatively small animals, most being under 1 metre in length, the largest being about 2 to 3 metres long. One of these, *Fulgurotherium australe*, has been discussed above, based on the first finds from Lightning Ridge in New South Wales. It has also been found in Victoria, again represented only by femurs.

The most complete hypsilophodont dinosaur known from Australia is *Leaellynasaura amicagraphica* (Rich and Rich, 1989). The name honours the Rich's daughter Leaellyn who helped her parents find the bones. *Leaellynasaura* was small, probably up to a metre in length, and is known from a well-preserved skull, isolated teeth and jaws, some leg bones (Fig. 7) and a good number of isolated bones including vertebrae. It was probably an agile little beast with very large eyes - perhaps a specialisation which helped *Leaellynasaura* see in the dark during the 3 months each year Victoria was then in darkness due to its close proximity to the South Pole (within 75°S). The teeth of *Leaellynasaura* are quite distinctive in having several ridges on both sides of the unworn cheek teeth.

The other hypsilophodont recently described from Victoria is *Atlascopcosaurus loadsi*, named after the Atlas Copco Corporation who generously donated earth moving and mining equipment to help excavate the bones (Rich and Rich 1989). *Atlascopcosaurus* is known from several isolated teeth and fragmentary jaw-bones (Fig. 7) which differ from those of other hypsilophodonts by their number of ridges and grooves on the teeth. Other bones found in the deposit could belong to *Atlascopcosaurus* but this cannot be established with certainty until more articulated skeletons come to light.

Atlascopcosaurus was probably about 2 or 3 metres long and had teeth well adapted for chewing on the tough coniferous plants that grew in the ancient cold river valley.

Apart from the three hypsilophodonts described above, there are various indeterminate bones of hypsilophodonts from southern Victoria which cannot be identified. Some of these could belong to additional new forms, but until the digging ends at Dinosaur Cove we will not know how to match up the isolated teeth and jaws with leg bone material. Recently a complete leg of a little hysilophodontid was found, and now much new material is helping solve the jigsaw of the three or more jumbled hypsilophodontid genera present in the fauna.

The theropod dinosaurs from these deposits are now represented by several forms. One foot bone represents an astragalus of *Allosaurus*, the same genus of meat-eating theropod that grew to 12 metres long in North America. The Australian *Allosaurus* (Fig. 8) was smaller and more robust, probably about 5 or 6 metres maximum length (Molnar, Flannery and Rich, 1981, 1985; see also Welles, 1983) and represents a late-surviving form living about 40 million years later than North American species.
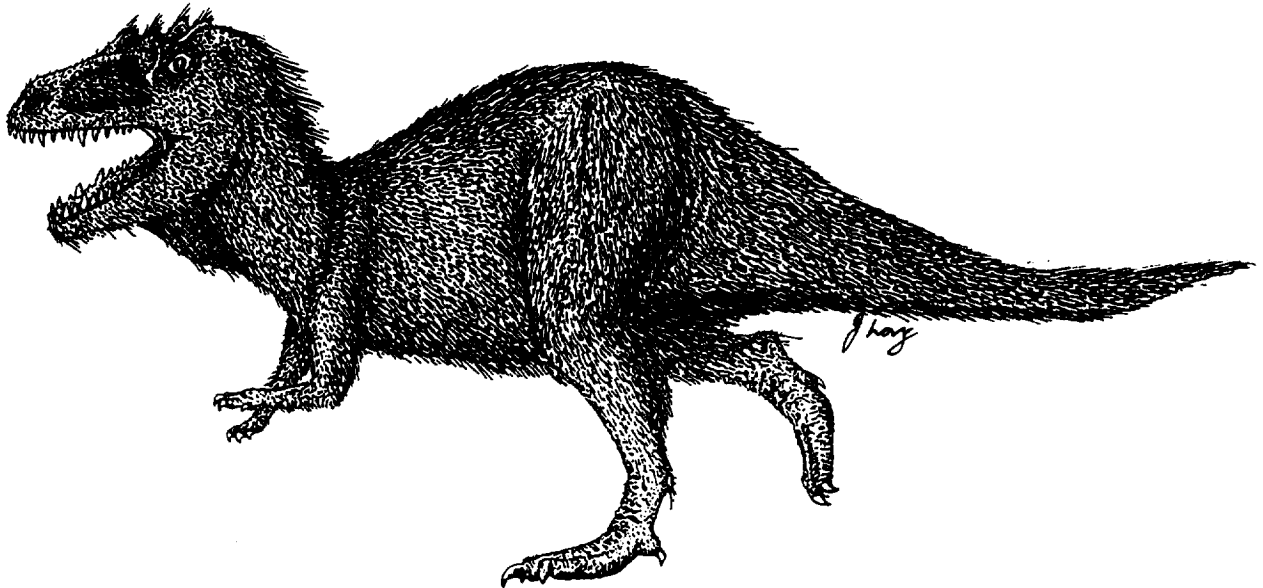
FIGURE 8. Imaginative reconstruction of a down-covered *Allosaurus* which lived in the cold polar climate of the Early Cretaceous of Victoria (after Long 1991).

The latest finds from Dinosaur Cove reveal that other theropods, like the slender ornithomimosaur *Timimus hermani* existed in Australia in the Early Cretaceous (Rich and Rich 1994). Other unidentified types of theropod bones, belonging in families not yet recognised in Australia have been found, and these will be vital in filling in some of the gaps in "missing dinosaur groups" from Australia (Rich and Rich, pers, comm).

One of the most unexpected discoveries from Dinosaur Cove is the bone of a ceratopsian from Australia. These dinosaurs, which include the large horned genera like *Triceratops*, are thought to have lived exclusively in North America and Asia, restricted to the Late Cretaceous. They were not expected to occur in Australia. However, an ulna found over the 1991/92 season (Fig. 9) appears to be close to that of a small, primitive ceratopsian, *Leptoceratops*. Although it is currently regarded with suspicion by its finders, Drs. Tom and Pat Rich, it is not unlikely that the group could have had Gondwana origins before becoming established in the northern hemisphere. An alternative explanation, and one that may not seem too far-fetched, is that the bone belongs to an exclusively Gondwanan group of ornithischians that occupied the same

niche as the ceratopsians, but is not closely related (i.e. convergent evolution, such as the identical body shapes seen in a dog and a marsupial wolf). We must await more finds of this fascinating beast to confirm its real identity.
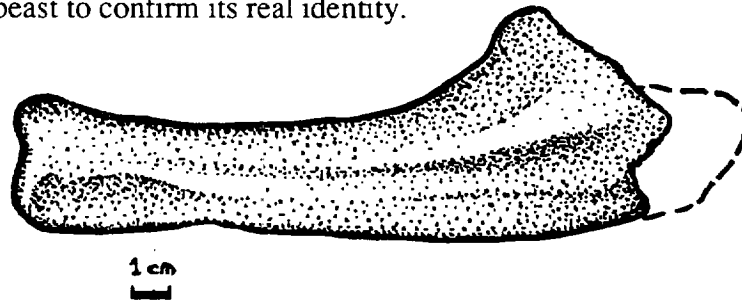

1 cm

FIGURE 9. Possible ceratopsian ulna *(? Leptoceratops)* from the Early Cretaceous of Victoria.

The most interesting thing about the Victorian dinosaur fauna is that chemical studies of the rocks using Oxygen isotopes have determined the ground temperatures when the animals lived (Rich *et al.*, 1988). The tests give an annual mean temperature less than 5°C, which is consistent with the estimated position of Victoria close to the South Pole at this time (latitude 75°-80°S). This means that not only did the dinosaurs live in a cold climate but they also had to endure darkness for up to three months per year. How did they cope with these harsh conditions?

One theory is that they were endothermic and could generate the needed internal heat from their own bodies, but in order to keep warm they would probably have required some specialized body covering, such as down feathers or even fur. The fact that pterosaurs had hair or fur indicates that other archosaurians, the reptile group including crocodiles, pterosaurs, dinosaurs and birds, already had the latent genetic ability to develop hair or fur covering. The diverse plant flora associated with the Victorian dinosaurs indicate that lush green forests of ferns and cycads covered the large river valley that formed as Australia began drifting away from Antarctica. Living with the dinosaurs were also the last known giant amphibians (labyrinthodonts) that died out elsewhere in the world some 50 million years earlier. This is also the case with *Allosaurus* which lived in the Jurassic Period of North America but survived longer in Australia to the latter half of the Early Cretaceous (Aptian-Albian age). The amphibians were not warm-blooded suggesting that perhaps enough sunshine came into the area to sustain a warm microclimate that supported cold-blooded life. Alternatively they may have been adapted to cold conditions like some present day Antarctic fishes that have anti-freeze enzymes in their blood to enable them to survive in subarctic waters.

Many scientists who have studied dinosaur physiology based on their skeletons, bone structures and reconstructed skeletons believe that they were most probably warm-blooded but not necessarily true endotherms. The larger the animal is, the less energy it requires to generate internal heat. A special term has been coined to explain this type of heat regulation in large animals - "gigantothermy" (Paladino and Spotila, 1992). It explains how a large, supposedly cold-blooded, reptile like the leatherback turtle can survive in freezing arctic waters whilst retaining a body temperature of over 25°C. In other words a gigantic dinosaur may have maintained a high constant body temperature without having the same in-built endothermic generator as mammals or birds do today.

Smaller dinosaurs would have had more difficulty managing a constant body temperature in these cold climates. A good argument for these little creatures being endothermic exists with the Victorian dinosaur fauna. Unlike bigger dinosaurs they

would have required a much higher metabolism to both generate and maintain enough body heat in cold polar temperatures. As most of the Victorian polar dinosaurs are small animals it seems likely that they may have used both endothermy and/or a modified form of ectothermy to maintain warm-blooded temperatures. The coexisting large labyrinthodont amphibians were possibly maintaining a constant body temperature through "gigantothermal" regulation similar to living forms of large marine turtles and large fishes, like White Pointer sharks *(Carcharodon carcharias)* .

The mystery of how the Victorian dinosaurs of the twilight zone managed to keep warm may never be solved, but at least we are slowly piecing together the fantastic story of what dinosaurs did inhabit Australia. New discoveries of dinosaurs from Australia are nonetheless of great scientific significance in determining the time of origin and migratory routes for some of the major dinosaur groups.

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The Extinction of Dinosaurs

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INTRODUCTION

That dinosaurs have been extinct for 65 million years is a well established fact of paleontology. But determining why dinosaurs (other than birds) became extinct has been a difficult problem for science.

The primary reason the extinction of dinosaurs is such a difficult problem is that dinosaur fossils are extremely rare. Paleontologists studying marine fossil shells can collect more individual fossils in a few days than all of the dinosaurs that have ever been collected.

There are intervals of geologic time during the age of dinosaurs from which virtually no fossils have been collected. Although dinosaurs lived and dominated the land for 140 million years during the Jurassic and Cretaceous periods, only about 2,100 complete dinosaur skeletons have ever been collected. Millions of dinosaurs were alive at any time during that long interval. However, our meager record of 2,100 articulated skeletons means that on average only one dinosaur skeleton has been found anywhere on earth for every 67,000 years of geologic time.

Of course, single bones or teeth of many more dinosaurs have been found, but even disarticulated bones are very rare. For example, a study (described below) involving large field crews over three summers found on average only one dinosaur bone for every 1,000 years of geologic time in the Hell Creek Formation, which is one of the richest sources known for dinosaur fossils.

Small wonder the history of dinosaurs is difficult to study! The scanty fossil record will always hamper scientists interested in these magnificent beasts by limiting the kinds of investigations that can be conducted.

THEORIES OF DINOSAUR EXTINCTION

Fifteen years ago most paleontologists believed dinosaurs had become extinct gradually. A gradual extinction fit the then-current models of evolution in which the more advanced mammals gradually replaced the more

primitive dinosaurs. Mammals were thought to have had advantages such as more active life-styles, the ability to regulate their temperature, and care for their young. We now know that many of these features were shared by the dinosaurs.

In 1980 Louis Alvarez and his son Walter Alvarez reported evidence that an asteroid (or comet) struck the earth 65 million years ago. They were working with rocks in Italy that had been deposited in a deep ocean. At the precise impact horizon they found evidence of the extinction event in the marine fossils.

They suggested that the asteroid impact produced a huge crater, and generated a dust cloud that enveloped the earth, blocking sunlight for nearly a year. They reasoned that loss of sunlight killed plants and removed the primary food source for animals. Ecosystems both on land and in the oceans collapsed. Dinosaurs were only one of many groups that suffered extinction.

THE EFFECTS OF AN ASTEROID IMPACT

When the dust cloud settled it formed a thin layer of clay over most of the earth. It is by far the most geographically wide-spread rock unit known on earth. The impact clay has been found in both marine and continental settings around the globe.

In dealing with the general public I find that the most misunderstood aspect of the asteroid extinction theory is an expectation that there should be massive bone beds at the extinction horizon. In fact, it is unlikely that any dinosaur bones will ever be found immediately beneath the impact-clay layer. Preservation of a dinosaur is a rare event. To preserve the bones they must be buried soon after death, commonly by floods or in stream channels. An inch of impact dust over a dead dinosaur would be insufficient for preservation. Those dinosaurs killed and covered by dust underwent a decay process that probably removed much of the dust covering the carcass.

In most terrestrial settings the impact-clay layer was removed by rain during the decades following the impact. On land the clay layer is commonly preserved only where it fell in swampy areas that were not subject to constant erosion. Since the clay layer is sporadically preserved on land, few dinosaur bones could have been preserved in close association with the impact clay.

Furthermore, dinosaurs would be no more abundant at the impact horizon than anywhere else in a formation. Even if the asteroid had not struck, all the animals living at that time would have died within about 100

years, and in the rock record 100 years is a very short period of time, commonly represented by only millimeters of strata.

Popular accounts of dinosaurs, for example museum dioramas or illustrations, depict dinosaurs in much greater abundance than they actually lived in nature. The artist usually wants to show several different animals, and to do this they must place animals in unrealistically crowded scenes (Fig. 1). An outcrop of the impact-clay layer is actually a line stretching across the hillsides. A geologic outcrop of a layer is like a string stretched through a modern landscape. If a string was stretched through a forest or the Serengeti Plain, how often would an animal be encountered? Of those few animals encountered, how many would actually be preserved in the fossil record? Finding even one dinosaur bone at the impact clay would be fortuitous indeed.
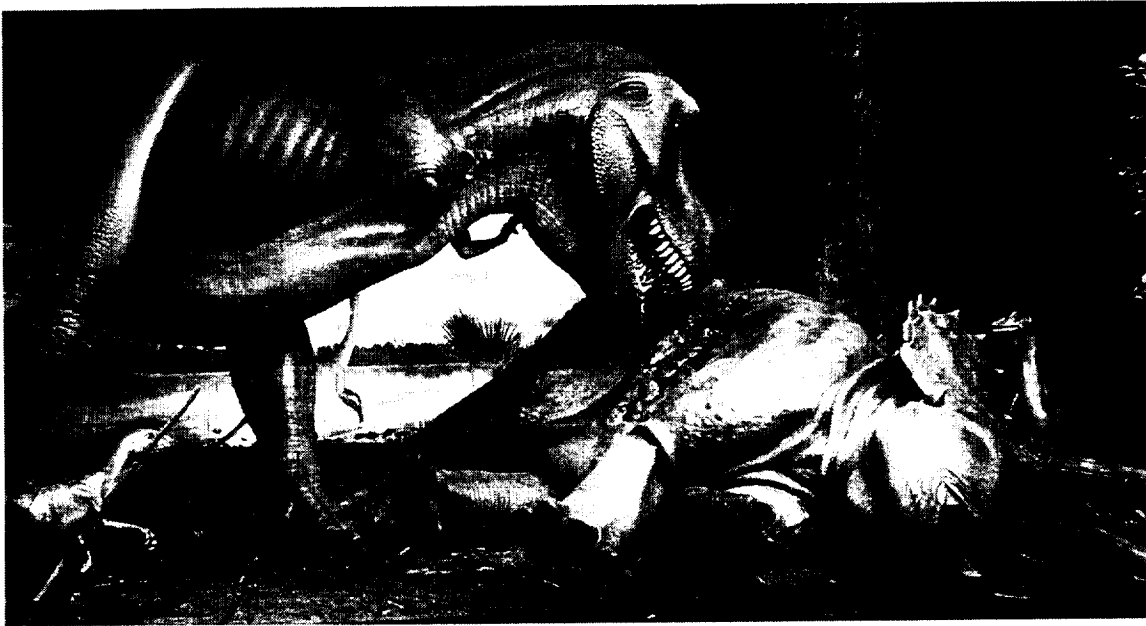
FIGURE *1*— Diorama at the Milwaukee Public Museum reproducing a scene based on fossils from the latest Cretaceous Hell Creek Formation. This community of animals became extinct at the end of the age of dinosaurs.

TESTING THEORIES OF EXTINCTION

Science has developed a methodology to choose between ideas such as gradual or sudden extinction. Theories are developed and then tested. When theories do not pass tests they are discarded. However, simply

passing a test does not prove a theory is true. Theories become accepted (but never proved) in science when they pass more and more tests, and when they demonstrate the ability to explain new observations.

GRADUAL OR SUDDEN DECLINE OF DINOSAURS?

One of the first tests of the asteroid impact theory was conducted by Robert Sloan and his co-workers in 1986. They recognized that the area of eastern Montana, western North Dakota and adjacent Canada was the only place on earth known to have abundant dinosaur fossils up to the extinction event. They assembled the records of known dinosaur fossil collections into a data base. They were able to plot the ranges of dinosaurs during the last 10 million years of the Cretaceous.

Rocks laid down about 10 million years before the end of the Cretaceous Period in Canada have produced some of the most diverse dinosaur fossil collections of any place on earth. Fossils in the Hell Creek Formation in adjacent Montana and North Dakota range up to the extinction event (evidence of the asteroid impact is present as the clay layer that formed when dust from the asteroid settled to earth.) The Hell Creek Formation has the second most abundant dinosaur fossil assemblage known.

Sloan et al. (1986) found fewer genera of dinosaurs in the younger rocks and reasoned that dinosaurs died out gradually. But statistical examination of their work revealed that although there were fewer kinds of dinosaurs in the younger rocks the differences were not statistically significant (Sheehan & Morse, 1986). More importantly, there were intervals of time between the two fossiliferous units when virtually no dinosaurs were present. Neither side was convinced by the others' arguments.

Keep in mind that rocks containing abundant dinosaur fossils are exposed in very few places on earth. If glacial till from the recent ice age had covered the rocks in Canada, the Hell Creek Formation would be the most abundant dinosaur beds known, and it would appear that dinosaurs were at their peak just before the impact. If the Hell Creek Formation were not exposed at the surface of the earth at this point in geologic time, the record of dinosaurs would make it appear that dinosaurs had been nearly extinct for millions of years before the impact.

The problem is that there are so few fossils and fossil-bearing rocks that it is not possible to accurately determine the ranges of clades of dinosaurs through time. There was not enough evidence available to Sloan and his co-workers to decide whether or not dinosaurs were declining gradually before their extinction.

A FIELD BASED TEST OF EXTINCTION THEORIES

Fortunately, other approaches are possible. In 1986 the Milwaukee Public Museum began a field investigation of the youngest interval studied by Sloan and his co-workers. We surveyed the Hell Creek Formation in Montana and North Dakota. To date this is the only field study of dinosaur bones that has been conducted with the expressed intent of testing the theories of dinosaur extinction.

Rather than examining the ranges of individual groups of dinosaurs, we looked for changes in the communities of dinosaurs. We found that there is no evidence for a gradual decline of dinosaur communities.

Using large search parties over three summers we surveyed the Hell Creek formation looking for dinosaur bones deposited during the last 2.1 million years of the reign of dinosaurs (Fig. 2). We looked for individual

FIGURE *2*—Field Crews searching for dinosaur fossils in the Hell Creek Formation near Glendive, Montana.
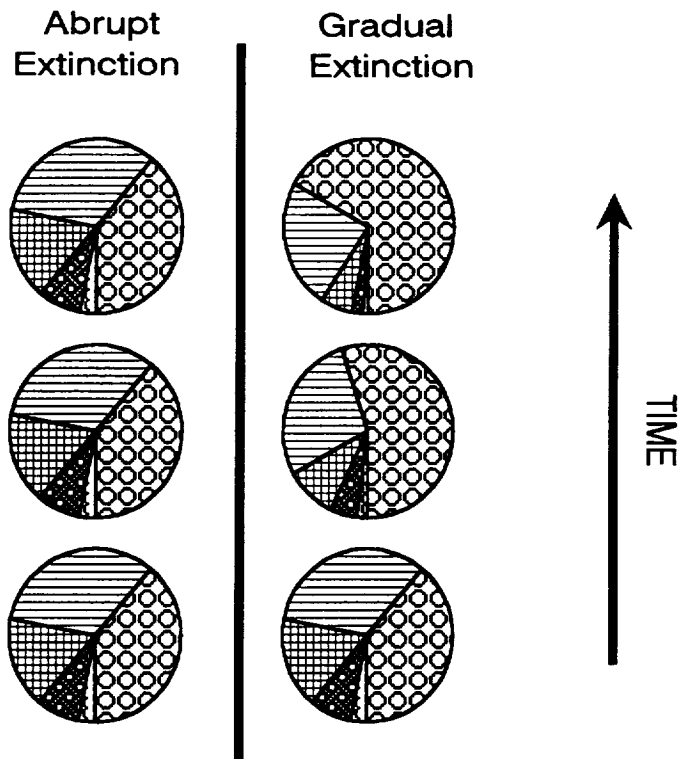
FIGURE *3*—Gradual decline or abrupt extinction? In these pie diagrams each segment represents the relative numbers of individuals of each family in a community. Communities are represented for three progressively younger intervals of time. If dinosaurs died abruptly, ecologic diversity should remain constant through time, and the relative proportion of groups in the community would not change through time. If dinosaurs declined gradually, ecologic diversity should decline through time, and a few groups should become more common while most groups become relatively less common. The pattern found (left and Fig. 4) supports a pattern of abrupt extinction.

bones which could be identified to at least the family of dinosaurs. We found ceratopsids, dromaeosaurids, tyrannosaurids, ornithomimids and several other groups (Fig. 1). Fossils of more than 2,000 individual dinosaurs were found, most only as single but identifiable bones.

We set up tests of both gradual and sudden extinction hypotheses. We divided the Hell Creek into three progressively younger parts, each about 700,000 years in length and compared the dinosaur communities from the three parts. We reasoned that if dinosaurs became extinct gradually, the relative proportions of different kinds of dinosaurs should have changed

through time. This was a study of ecological diversity that is akin to studies by modern ecologists examining deteriorating ecosystems. Ecologists have found that when communities of animals are in trouble most groups begin to die out, while a few groups become dominant, resulting in a decline of ecological diversity (Fig. 3).

We designed two tests. If dinosaurs died out gradually, ecological diversity should have declined through the last 2 million years of the Cretaceous (Fig. 3, right). If the dinosaurs died out suddenly, ecological diversity should be unchanged during the three, progressively younger, intervals of the Hell Creek Formation (Fig. 3, left).

We found strong, statistically reliable evidence that ecological diversity of dinosaurs did not change during the last 2 million years of the Cretaceous (Fig. 4). The relative number of individuals of each group remained constant. For example, the herbivorous ceratopsids were more common than the carnivorous tyrannosaurids, but more importantly, the relative numbers of individuals of each group remained constant through time.

Ecological diversity was not changing, and we could reject the gradual extinction hypothesis. The data are consistent with a sudden extinction hypothesis, such as an asteroid impact, but do not prove the hypothesis.

Position in Hell Creek Formation	Shannon Index (-H') standard error
Upper 1/3	1.11
	0.11
Middle 1/3	1.21
	0.09
Lower 1/3	1.15
	0.19

FIGURE 4—Ecological diversity (expressed using the Shannon Index) of dinosaurs from the lower, middle and upper Hell Creek Formation. Each interval represents successive 700,000 year intervals prior to the extinction event. These data are for fossils collected from sediments deposited in stream channels (complete data in Sheehan, et al. 1991). The relative proportion of families remained statistically similar through the Hell Creek interval.

Several criticisms have been directed at our study, but they can be refuted. One is that since we did not study articulated specimens it is possible that our study was biased by bones that had been reworked from underlying layers. This would only be important if relatively large numbers of bones were involved. Reworking of teeth, which are more resistant than other bones, might present a problem, but very few teeth were used in our study. Beds above the Hell Creek Formation represent the period immediately after the extinction of dinosaurs, and while several teeth of dinosaurs have been found in these beds, bones of dinosaurs are extremely scarce compared to those in the Hell Creek. Thus, reworking of dinosaur bones was uncommon, and reworking is not a problem for our study.

Another criticism has been that we used families of dinosaurs rather than species. Families were used because of the very rare occurrence of fossils. While it is possible to identify many bones to family it is often not possible to determine the actual species. But this is not an issue, because we were examining ecological diversity not the ranges of individual species.

Some workers have suggested that studying families rather than species could mask the extinction of a species if there were more than one species in the family. This criticism misunderstands the study of ecological diversity, which is based on the relative number of individuals of all dinosaurs. Extinction of a species would be apparent because the relative number of individuals of the family to which the species belongs would decline compared to the abundance of other families.

There has also been a suggestion that there could have been a gradual decline over the last 700,000 year interval. This idea reframes the gradual extinction hypothesis from one covering the last several million years of the Cretaceous (Sloan, et al., 1986) to a gradual extinction covering only the last few hundred thousand years. If true the gradual extinction could not have occurred during the entire final 700,000 years, because a gradual decline over the entire final interval would have resulted in a significant decline in ecological diversity compared to the earlier intervals. A gradual decline over the last 100,000 might be possible in our data, although there is no evidence for it. While 100,000 years is a long interval of time, it pushes credibility to suggest that dinosaurs dominated earth for 140 million years, only to decline gradually in the final 100,000 years, just before an asteroid struck the earth.

OTHER EXTINCTION HYPOTHESES

Over the years many hypotheses have been suggested for the extinction of dinosaurs. Recently such ideas as fragmentation of the dinosaurs' habitat or spread of disease during dinosaur immigrations have received much

attention. These hypotheses will need to be tested in the future. But one overriding feature of the extinction event is that the extinction took place both on land and in the oceans. Any event that caused the extinction of dinosaurs must be tied to the simultaneous extinction of many other animals both on land and in the oceans around the world.

ECOLOGICALLY SELECTIVE EXTINCTION

Effective scientific hypotheses are able to explain new information. Another test of the asteroid impact hypothesis involves comparing the ecology of survivors with the ecology of groups that became extinct. This test centers on the idea that sunlight was blocked from the earth for several months. The presence of a dust layer over much of the earth is consistent with this idea. Recent work in the southern hemisphere suggests the dust cloud may not have affected high southern latitudes. But over most of the world the presence of a dust cloud would have cut off photosynthesis. Green plants would have died. There was an interval, probably more than a year,
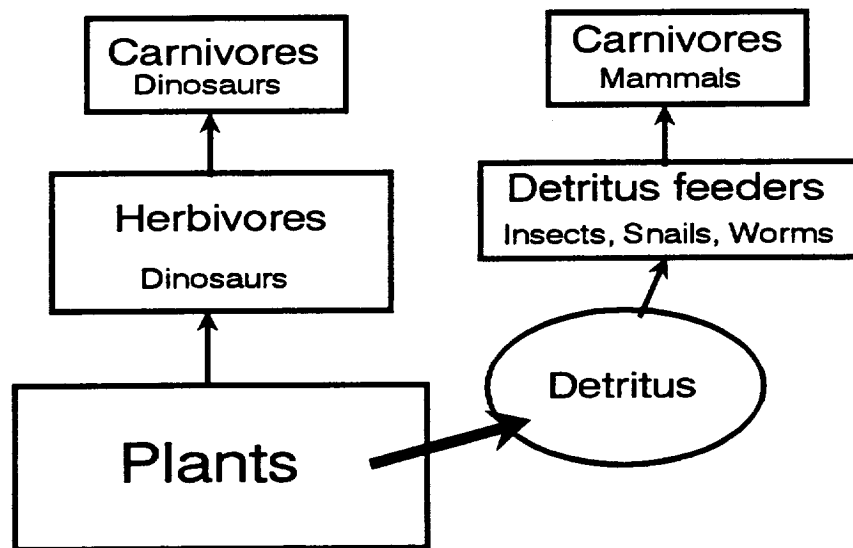
FIGURE 5—Cretaceous Food Chains. Lower levels in food chains serve as food for upper levels. Most animals live in food chains that depend directly on living plants (left). Some animals live in food chains based on detritus which is dead plant and animal matter (right). At the end of the Cretaceous loss of sunlight for many months may have stopped production of living plant material, causing extinction of animals in food chains based on living plants. Animals able to live in detritus based food chains may have preferentially survived the temporary loss of sunlight.
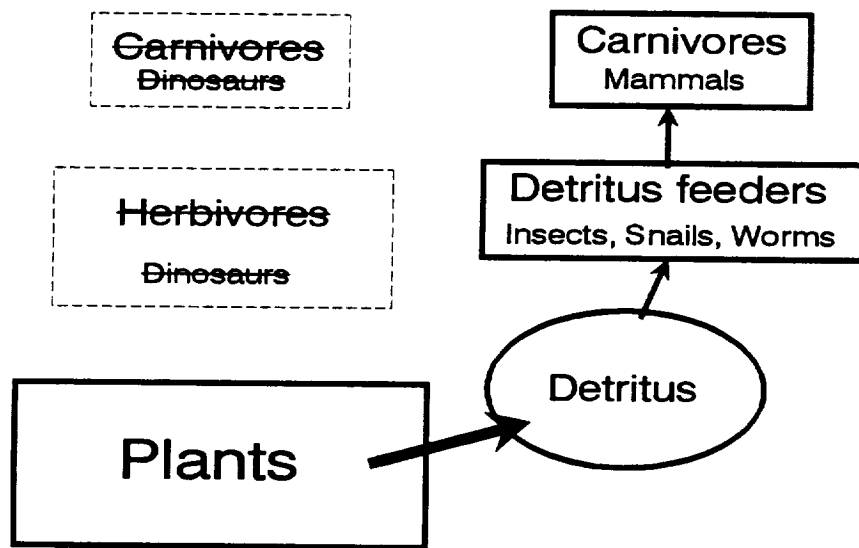
FIGURE *6*—Post-impact food Chains. When the dust from the impact
settled, sunlight returned and plants regenerated from seeds and root
systems. Dinosaurs, which had been in food chains requiring green
plants for food, had become extinct. Animals in food chains based on
detritus feeding (and animals able to switch to detritus based food
chains) preferentially survived. In the early Paleocene large bodied
terrestrial herbivores and carnivores were missing. It would be millions
of years before mammals radiated to occupy these vacated life styles.

when green plant food was unavailable, and animals in food chains directly
dependent on green plants would have succumbed. However, animals in
food chains that were not directly dependent on living green plant matter
might have been able to survive.

Simplified examples of food chains are given in Figures 5 and 6. The key
to survival may have been that some animals were able to feed in food
chains that depended on detritus--the accumulation of dead plant and
animal matter. The animals living in a dead log or in the dead plant litter
of the forest floor are examples. Sheehan and Hansen (1986) suggested that
this pattern is present in the fossil record on land, and they, along with
Arthur et al. (1987) and Rhodes and Thayer (1991), found the same pattern
in the oceans.

David Fastovsky and I were presented with an unusual opportunity to
examine this problem, once again using the fossil record from the Hell Creek

Formation. Our prior study was designed exclusively to examine dinosaurs in the Hell Creek Formation. But in 1990 David Archibald and Laurie Bryant published an analysis of the fossils of all animals found in both the Hell Creek Formation and the overlying, post-extinction Tullock Formation.

By dividing these fossils into those that lived in streams and lakes, as opposed to those living on land, Sheehan and Fastovsky (1992) found a remarkable pattern (Fig. 7). Of the species of animals living on land 88% became extinct, but only 10% of the species of animals living in streams and lakes became extinct.
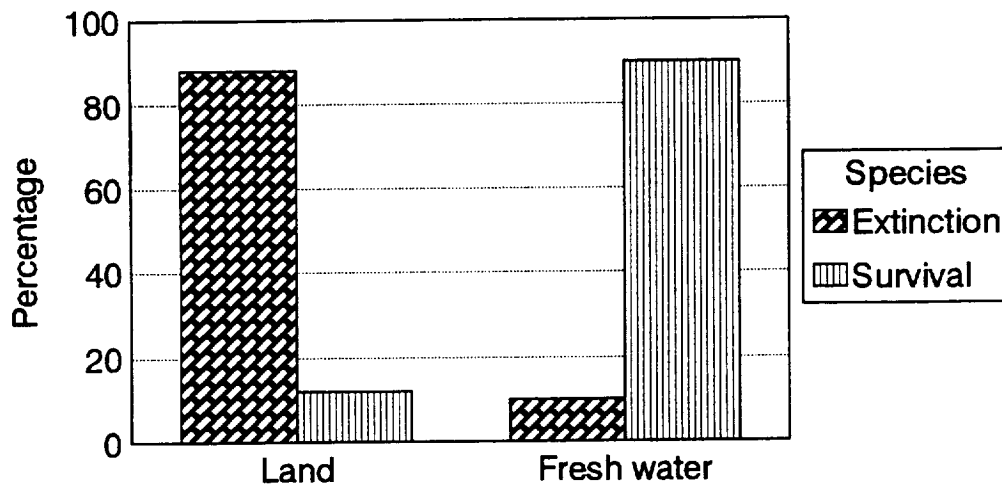
FIGURE 7—Survival of species of Hell Creek animals across the extinction event. Animal species in streams and lakes suffered little extinction. High levels of extinction occurred in animals living on land. (After Sheehan and Fastovsky, 1991.)

The patten of extinction and survival was a familiar one. Few animals in streams and lakes depend exclusively on living plants. Most of the food originates as detritus which washes in from the land. But on land most animals are in food chains dependent directly on living plant matter. Again the asteroid impact passes the test.

SURVIVAL OF MAMMALS

Mammals dominate the modern land just as dinosaurs did during the age of dinosaurs. But during the age of dinosaurs, the ecology of mammals was much less diverse than it is today. Many mammals were insectivorous, feeding on insects, snails, and worms in the forest litter. Their lowly position in the detritus-based food chains (Fig. 6) may have allowed mammals to survive while dinosaurs became extinct.

Following the extinction of dinosaurs the land was a very unusual place. Plants soon recolonized the world, germinating from seeds and growing from root systems. But there were no large herbivores or carnivores. It would be millions of years before mammals evolved into large plant eaters or carnivores. The asteroid impact eliminated an entire ecosystem and allowed a new one to evolve. Without the sudden, selective extinction of dinosaurs, mammals would not have diversified, and humans would not be pondering this cataclysmic event.

ACKNOWLEDGMENT

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Chicxulub Structure: A Volcanic Sequence of Late Cretaceous Age

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INTRODUCTION

The present Cretaceous/Tertiary extinction debate started with findings by Alvarez et al. (1980) of enhanced levels of iridium at K/T sections in Italy, Denmark and New Zealand. They postulated that the iridium was extraterrestrial in origin and related to a 10 km diameter asteroid impact which would have produced a crater some 200 km in diameter. They further suggested that a giant dust cloud would have been injected into the stratosphere from the impact with a residence time of several years and that the resulting darkness would have suppressed photosynthesis with a consequent elimination of succeeding members in the biological food chain — ergo, a mass extinction event.

The Alvarez hypothesis was simple, straightforward, and dramatic and it was argued by an eminent scientist. As Australian journalist Ian Worden put it in an issue of *The Canberra Times*: "To connect the dinosaurs, creatures of interest to but the veriest dullard, with a spectacular extraterrestrial event like the deluge of meteors ... seems a little like one of those plots that a clever publisher might concoct to guarantee enormous sales. All the Alvarez-Raup theories lack is some sex and the involvement of the Royal family and the whole world would be paying attention to them."

From the very beginning objections were raised by the paleontologists to the "lights out" hypothesis, as it was referred to. It would have represented a very short lived event in the geological record and there was no large dinosaur bone pile or shellfish collection to accommodate the hypothesis. The paleontological studies — be they of dinosaurs, shallow water shellfish, or ocean plankton — showed that the extinctions were neither instantaneous nor as near total as postulated but occurred sequentially over a period of 10,000 years and longer — still a catastrophic event in geological terms but on a longer time scale.

As has happened from time to time in other geological controversies, matters became rancorous. Paraphrasing another, earlier physicist, Lord Kelvin, Luis Alvarez lashed out at the paleontologists. In an issue of *The New York Times*, Alvarez said, "They're really not very good scientists. They're more like stamp collectors."

But a continuing collection of what we might call "geophilatelic insights" nonetheless raised questions about the impact hypothesis. The hypothesis called for the creation of a dust cloud 1000 times greater than that produced by the eruption of Krakatoa. But Kent (1981) pointed out that 75,000 years ago the eruption of the still larger volcano Toba sent up a dust cloud estimated to be at least 400 times that of Krakatoa. Yet no abnormal rate of extinction occurred after the Toba eruption.

Then, the very basis for their hypothesis that the iridium anomalies had to be of extraterrestrial origin came into question. Zoller et al. (1983) and Olmez et al. (1986) discovered that fine particle, volcanic emanations collected over the volcano Kilauea in

Hawaii were enriched in iridium by a factor of 10,000 over that of normal Hawaii basalts. Koeberl (1989) found that volcanic dust bands in Antarctic ice cores are enriched with values of 4-7 parts per billion (ppb), comparable to what is found at K/T sections. Felitsyn and Vaganov (1988) found iridium levels of 1-4 ppb for fine volcanic ash from acidic volcanoes in Kamchatka. And Toutain and Meyer (1989) found iridium levels of 4-8 ppb in sublimates from eruptions of a mantle plume volcano on Reunion Island. These were extraordinarily important findings; for the K/T anomalies are, indeed, associated with fine clay particles. Had they been made prior to the original Alvarez article, that article might have had a different emphasis.

But by the time of these discoveries the band wagon was rolling. There were dreams of fame and glory. This was going to be the greatest geologic paradigm since plate tectonics — maybe even greater. And research funds were available. What better way had NASA to justify its large expenditures than searching for "things" from outer space that might be a veritable threat to the very existence of human beings on Earth.

And the rancor increased in level. Taking a page from Luis Alvarez some of his lieutenants became arrogant, vicious, and unmitigated zealots of the impact hypothesis. Objective research took a back seat to subjective discourse. The unbelievers had to be forcefully reeducated and those who could not see the light had to be drummed out of the geological profession.

If the iridium argument was fading away from the impact proponents, another one came along to take its place — planar lamellar substructures in quartz grains. They are found at some K/T sections; they are also found at a large number of other geologic settings around the Earth. They are sometimes referred to as "shock lamellae", but this is a misnomer since not all of them are of shock origin.
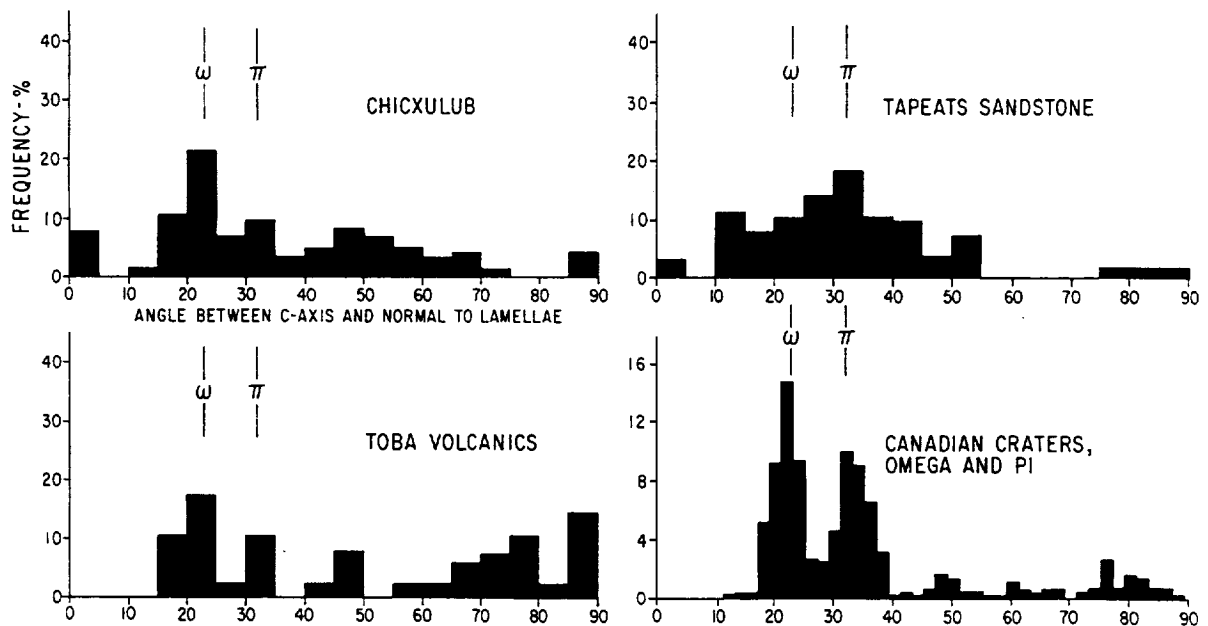

Figure 1. Orientation plots. (A) Chicxulub structure, 71 sets, Sharpton et al., 1992. (B) Toba volcanics, 36 sets, Carter, et. al., 1990. (C) Tapeats sandstone, 58 sets, Lyons et al., 1993. (D) Ten Canadian craters, omega and pi orientations, 687 sets, Robertson et al., 1968.

Both single and multiple sets of lamellar features in quartz grains can be produced in shock experiments and are observed at known impact sites; they can also be produced in strain rate experiments where the differential stress is gradually increased over several hours and are observed at known tectonic and explosive volcanic sites. The former are strictly planar and parallel and generally conform to rational crystallographic orientations in the quartz crystal structure, generally basal (0°), omega (23°), and pi (32°). The latter can also be planar and parallel but sometimes show slight to moderate curvature with lamellar bifurcations and variable lamellar widths. Their orientations show a variety of forms with, in general, a broader angular distribution than that of impact generated lamellae (Lyons et al., 1993).

Plates IA and IB show multiple intersecting lamellae from a strain rate experiment and from the Tapeats sandstone of tectonic origin. For comparison, Plates IC and ID show multiple intersecting lamellae from a shock experiment and from the Clearwater Lakes impact site. Figures 1B, 1C, and 1D show orientation plots from the Toba volcanic eruption, Tapeats sandstone, and ten Canadian impact craters with preferred omega and pi directions.

If all the lamellae observed at a natural setting are planar and parallel and conform to rational directions in the quartz crystal, they are probably of impact origin. If some are curved, show bifurcations, and have variable lamellar widths with a broad angular distribution, they are probably of tectonic or volcanic origin. But there is a large grey area in between. We shall return to this subject when we discuss the Chicxulub structure.

CARIBBEAN CAPER

We now go on to the recent studies in the Caribbean — the Caribbean caper. The reader should be forewarned that we are now entering never-never land; put on your rose-colored glasses. Some have referred to these studies as pathological in the sense that that word has been applied to N rays, polywater, and more recently cold fusion. It has been the inventing of a new geology to fit preconceived conclusions. It has called on a *deus ex machina* as difficulties have arisen and the situation may demand. But in the end interpretations have to answer to the data — all the data.

A boulder bed in Cuba was reinterpreted as an "impact ejecta blanket" (Bohor and Sietz, 1990). But this is not the case. Iturralde-Vinent (1992) of the National Museum in Havana studied the geology of the deposit in the field and found the boulders to be of local, in situ weathering origin — representing an exfoliation process, a conclusion confirmed by others (Dietz and McHone, 1990).

A K/T section in Haiti was reinterpreted to be of impact origin and to contain tektites. Subsequent studies belie this interpretation (Lyons and Officer, 1992; Jéhanno et al., 1992; Officer and Lyons, 1993). (1) The Haiti section consists of two to six different graded calcareous debris flows, some of which are separated from one another by several centimeters of bioturbated limestone. (2) The section is characterized by abundant palagonite alteration products. The palagonite-smectite spherules are characteristic volcanic glass alteration products. An outstanding characteristic of known tektites is that they are resistant to devitrification and alteration. (3) Some of the spherules are broken and those that are broken are invariably hollow; some of these have secondary microspherules on their interior. No known tektites show such a complex morphology. (4) The black glass particles are of an andesitic-dacitic composition. Known tektite glasses have a much higher silica content. (5) The glass particles are vesicular. Volcanic

A

B

C
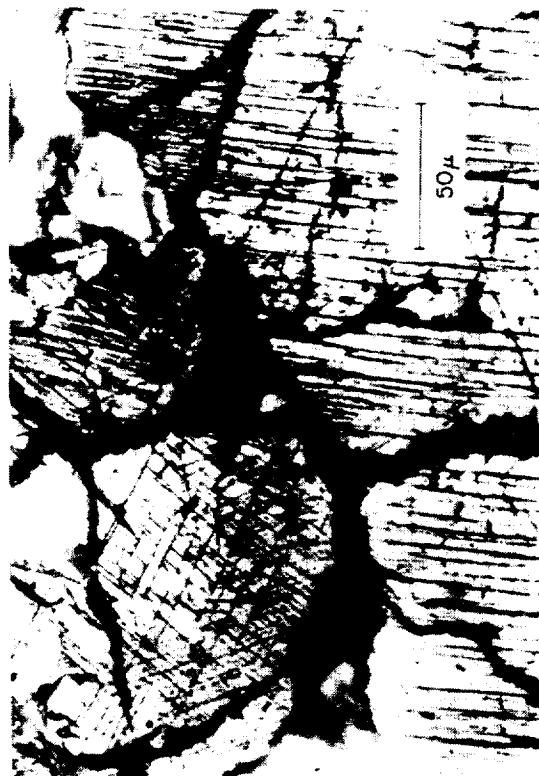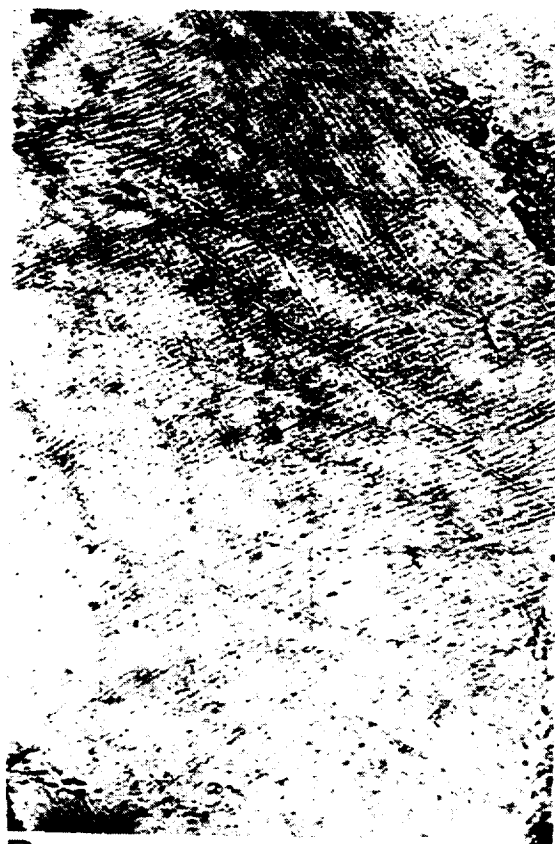
D

Plate I - Lamellae in quartz grains. (A) Strain rate experiment results, northeast and northwest trending lamellae, scale bar 100 μm, Heard and Carter, 1968. (B) Tapeats sandstone, several sets of intersecting lamellae, length of photograph 650 μm, Lyons et al., 1993. (C) Laboratory shock generated lamellae, Sclar et al., 1968. (D) Clearwater Lakes impact site, omega orientations, scale bar 100 μm, Carter, 1968.

glassses can be vesicular; tektites are characteristically devoid of vesicles and bubbles. (6) The black glasses do not contain crystals. Tektites are devoid of crystals as are some volcanic glasses. (7) Accretionary lapilli are present. Some of the accretionary lapilli contain black glass particles as well as smectized clasts of a differing composition. There are no known tektites with such a complex structure. (8) The rare yellow glasses with a high calcium content contain microcrystals of melilite. Tektites are devoid of microcrystals. (9) The iron reduction state of the glasses is characteristic of volcanic andesites and not the highly reduced state found in tektites: $Fe^{3+}/Fe^{2+} = 0.7 \pm 0.1$ for Haiti black glasses, 0.67 for andesites, and 0.03-0.15 for tektites. (10) There is no lechatelierite, a high temperature fused form of quartz characteristic of tektites, in the Haiti glasses. And (11) the presence of sulfur in the rare yellow glasses, implying a temperature not exceeding 1300°C, is inconsistent with the high temperature formation of tektites. If one wishes to interpret the Haiti deposit to be of impact origin, it requires the assumption of abundant tektite alteration products and tektite glasses of a composition and vesicularity, never before observed, and a formation process at lower temperatures than previously associated with tektites.

Deep Sea Drilling Project (DSDP) Sites 536 and 540 in the Gulf of Mexico were reinterpreted as impact generated, tsunami deposits (Alvarez et al., 1992). Subsequent studies have shown that there is a hiatus at K/T time for these DSDP sites and that a 3 m thick layer at DSDP Site 540 is of volcanoclastic origin (Keller et al., 1993), in agreement with the original lithologic description given for this layer (Buffler et al., 1984).

A K/T section at Mimbral in northeastern Mexico has been interpreted as representing proximal impact ejecta and an impact generated, tsunami deposit (Smit et al., 1992). Subsequent studies at Mimbral and two other adjacent sites have shown that it is a channel deposit with three lithologically and mineralogically distinct units separated by disconformities (Stinnesbeck et al., 1993). The units include, from bottom to top, a spherule rich layer, a laminated sandstone, and a rippled sand and shale layer. Some of the spherules contain apatite concretions whereas others contain rounded clasts of limestone or foraminiferal tests filled with glauconite. Quartz grains with multiple sets of lamellae are rare and are found within as well as above and below the channel deposit. The lamellae are curved and are of probable tectonic or volcanic origin.

CHICXULUB STRUCTURE

This reinterpretation of K/T sections in the Caribbean and Gulf of Mexico then led to a frantic search for circular structures around 200 km in diameter that might be identified as the hypothesized K/T asteroid impact site. Four sites have so far been suggested.

The Isle of Pines southwest of Cuba (Bohor and Seitz, 1990) and the Massif de la Hotte on the southern peninsula of Haiti (Maurrasse, 1990) were suggested as K/T impact sites. There is no evidence for such at either site and both suggestions have since been discarded (Officer et al., 1992).

The Colombian Basin in the western part of the Caribbean Sea was suggested as a possible impact site (Hildebrand and Boynton, 1990). The basement topography there has a semicircular aspect with a diameter of 300 km. Unfortunately nearby DSDP sites and continuous seismic profiling lines show Upper Cretaceous sedimentary strata overlying the basement (Officer et al., 1992). Thus, it is a stratigraphic impossibility for the topography of the underlying basement to have been formed by a later event of K/T age.
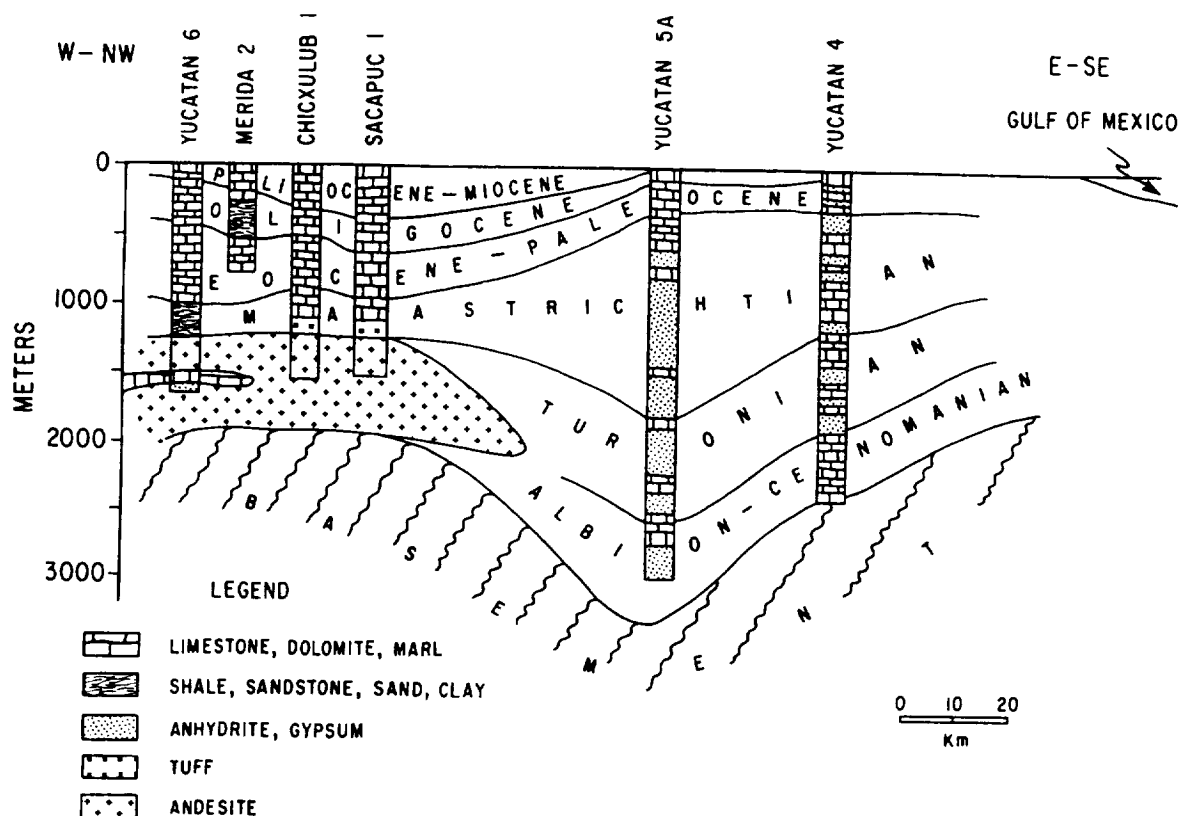
Figure 2. Inferred correlation from well control along an east-west section in the northern part of the Yucatan Peninsula. The Chicxulub structure is to the left in the diagram. From Lopez-Ramos (1975).

The fourth suggestion is the Chicxulub structure on the northwestern coast of the Yucatán Peninsula (Hildebrand and Boynton, 1990; Hildebrand et al., 1991). As defined by magnetic and gravity anomalies, it is a circular structure about 200 km in diameter. Drilling has shown that the anomalies at Chicxulub are related to an andesitic body at a depth of 1200-1300 m (López-Ramos, 1973, 1975).

Most of what follows herein has been taken from Meyerhoff et al. (1994). As indicated in Fig. 2, the wells on the structure penetrated an orderly sequence of Pliocene-Miocene, Oligocene, Eocene-Paleocene, and Late Cretaceous sediments with Maastrichtian microfauna above and middle Campanian fauna below, overlying the volcanic sequence. For the Chicxulub No. 1 well the top of the Maastrichtian was cited at a well depth of 920 m and the top of the andesite at 1270 m for 350 m of Cretaceous strata; for the Yucatán No. 6 well the top of the Maastrichtian was cited at 1000 m and the top of the andesite at 1260 m for 260 m of Cretaceous strata. (In the Meyerhoff et al. article the 350 m was incorrectly attributed to the Yucatán No. 6 well rather than to the Chicxulub No. 1 well.)

The part of the well log covering the volcanic sequence in the Yucatán No. 6 well is repeated here as Fig. 3. Taking bentonite as indicative of weathering and a halt in volcanism, the log shows a sequence of at least six major volcanic events — unit O, units L and K, units I and H, units G and F, units E and D, and unit B. Within the sandstone of

unit C there are also three bentonitic intercalations. Fossiliferous Upper Cretaceous strata lie both *above* and *within* the volcanic sequence, and the well terminated in anhydrite of Cretaceous age. Moreover, the Chicxulub volcanics are part of a well known Late Cretaceous igneous province surrounding the Gulf of Mexico.

The critical cores within the andesitic interval are cores N14 through N22. Their descriptions at the time they were recovered are as follows: N14 and N15, bentonitic breccia of andesitic or basaltic composition; N16 through N20, basaltic andesite or andesitic basalt; N21, *interbedded* limestone with Late Cretaceous microfossils, volcanic breccias, and andesite; N22, mainly anhydrite and limestone of Turonian age. It is quite possible that the volcanic sequence continues to greater depths than that at which the Yucatán No. 6 well terminated and to older ages, for there are numerous pyroclastic beds interlayered with anhydrite and limestone of Albian-Cenomanian and Turonian ages in the Yucatán No. 1 well located 150 km southeast of the Chicxulub structure. There is *no* similarity between this well log and the simple succession encountered in impact melt sheets.

For a structure the size of Chicxulub, 200 km diameter, the excavation depth, were it of impact origin, would have been 10 km or greater. All of the bedded sedimentary sequences of Cretaceous age and a substantial part of the underlying crust would have been obliterated by a presumed K/T impact.
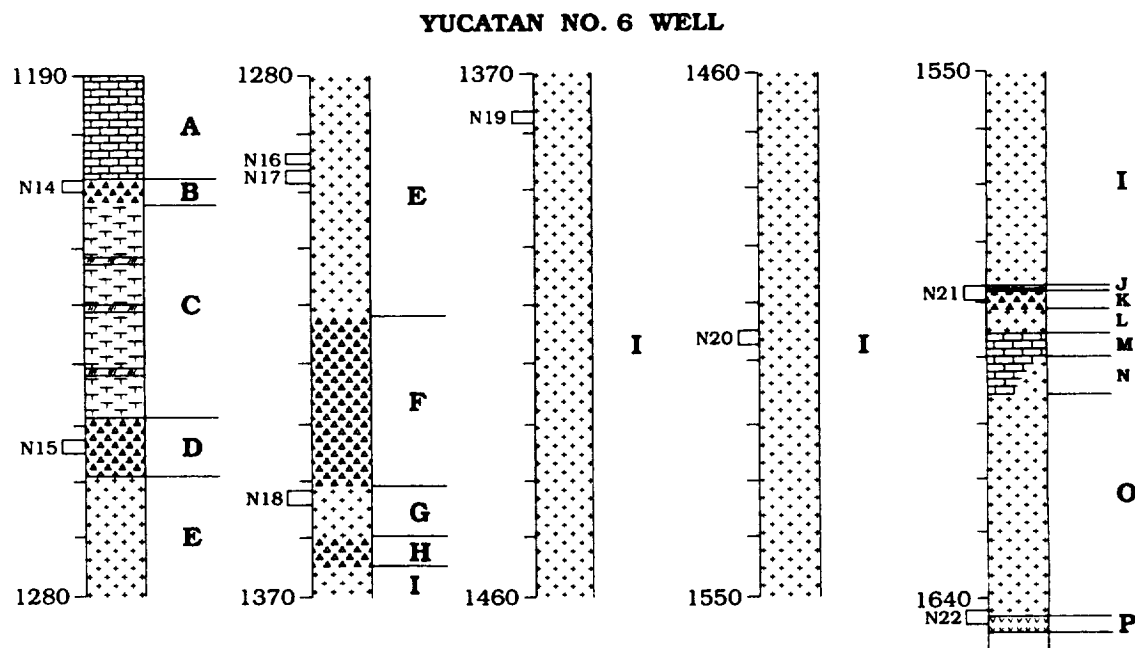
YUCATAN NO. 6 WELL

Figure 3. Yucatan No. 6 well log. Depths in meters; well bottomed at 1645 m. N14-N22 mark depths at which cores were taken. Lithologic descriptions: A- Upper Cretaceous (Campanian) limestone; B - emerald-green bentonitic breccia; C - fine to medium grained, gray-green sandstone containing thin intercalations of light brown to buff and gray bentonite; D - siliceous bentonitic breccia of light green, dark gray to black and reddish brown color, including small to medium sized and a few large fragments of limestone; E - andesite; F - bentonitic breccia; G - andesite; H - bentonitic breccia; I - igneous rock, extrusive andesite; J - limestone; K - volcanic breccia; L - andesite; M - white crystalline limestone, very fine, saccharoidal; N - cream white limestone, very fine crystalline with traces of andesite; O - andesite; and P - anhydrite. Lithologic descriptions are as given on the original well log by J. Maldonado.

Quartz grains with both single and multiple sets of lamellae do occur in the Chicxulub rocks but they are quite rare. Quezada Muñeton et al. (1992) showed an example of lamellar features in a quartz grain from core N14; the lamellae have slight curvature with bifurcations, and the lamellar widths are variable. Sharpton et al. (1992) included an orientation plot of N14 lamellae, repeated here as Fig. 1A; the plot shows a modest peak at omega and pi and a substantial distribution at angles from 40° to 90°. Plate II shows two quartz grains from core N10 of the Chicxulub No. 1 well with single sets of northwest trending lamellae. In both quartz grains the lamellae are curved and have variable lamellar widths. Both the form and the angular distribution are characteristic of tectonic or volcanic lamellae.

There have also been later thermal events in the Chicxulub volcanic sequence. Core N10 from the Chicxulub No. 1 well shows fine scale replacement of plagioclase by microcrystalline albite. This indicates temperatures in excess of 200°C; the upper temperature limit could be several hundred degrees higher. Sharpton et al. (1992) analyzed ten glass samples for $^{40}Ar/^{39}Ar$ ages. Nine of the samples, which were from the cores N14, N17, and N19 of the Yucatán No. 6 well, gave unreliable age spectra ranging from 58.2 to 65.6 Ma; and Sharpton et al. concluded that this was the result of low temperature alteration of the samples. They considered that the tenth sample, from core N10 of the Chicxulub No. 1 well, gave a reliable age of 65.2 Ma. We suggest that as with the Yucatán No. 6 samples, this sample also represents an alteration age in accord with the observed albitization in core N10. Much the same $^{40}Ar/^{39}Ar$ age results were obtained by Swisher et al. (1992) — unreliable ages for the Yucatán No. 6 samples and an age of 65.1 Ma for the Chicxulub No. 1, core N10 sample. A pertinent caution to such age determinations comes from the study of cores from the Manson structure in Iowa, once considered a K/T impact site. Recent age determinations of 74 Ma from sanidine replace the previous glass age of 65 Ma (Izett et al., 1993).

Objections to the publication of the drilling results were soon to appear (Marin et al., 1994). They concentrated exclusively on two cores, N12 and N13, from the Yucatán No. 6 well. These two cores are above the interval shown in Fig. 3. Core N12 is at a depth of 1000-1003 m. They find that it contains Danian fauna, an observation which had previously been made by Hildebrand et al. (1991). The wellsite paleontologists placed the K/T boundary at 1000 m. At the time the Yucatán No. 6 well was drilled, 1966, the Danian was considered to be the uppermost part of the Cretaceous rather than the lowermost part of the Tertiary as it is today. There is no conflict between the original paleontological findings and these more recent determinations.

Core N13 is at a depth of 1100-1103 m. It was originally logged as a green bentonitic sandstone. Marin et al. have chosen to reinterpret it as an "impact breccia". They go on to state, on the basis of these two cores only, that core N12 is "immediately above the impact rocks". This is incorrect. Examination of the electrical log, Fig. 4, shows that the lithology of the interval from 1087 m to 1107 m, which includes core N13, is very different from the beds above and below this interval. Therefore, the description of core N13 does not apply to the cuttings from the beds either above or below it which consist of gray calcareous marine shale, marl, and carbonate with Campanian-Maastrichtian fauna. Core N13 represents an isolated interval within the Late Cretaceous sequence.
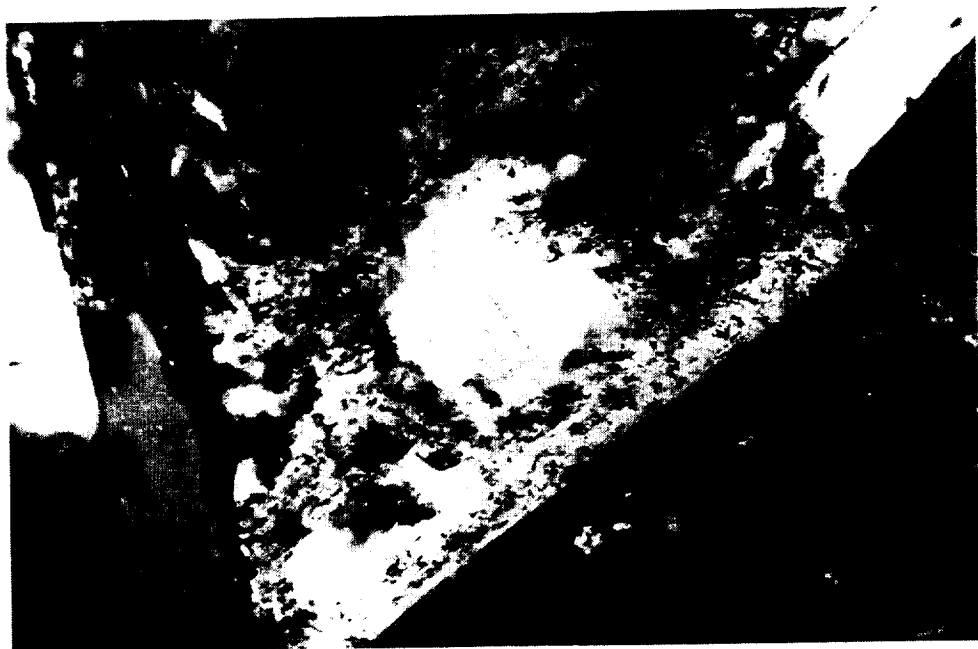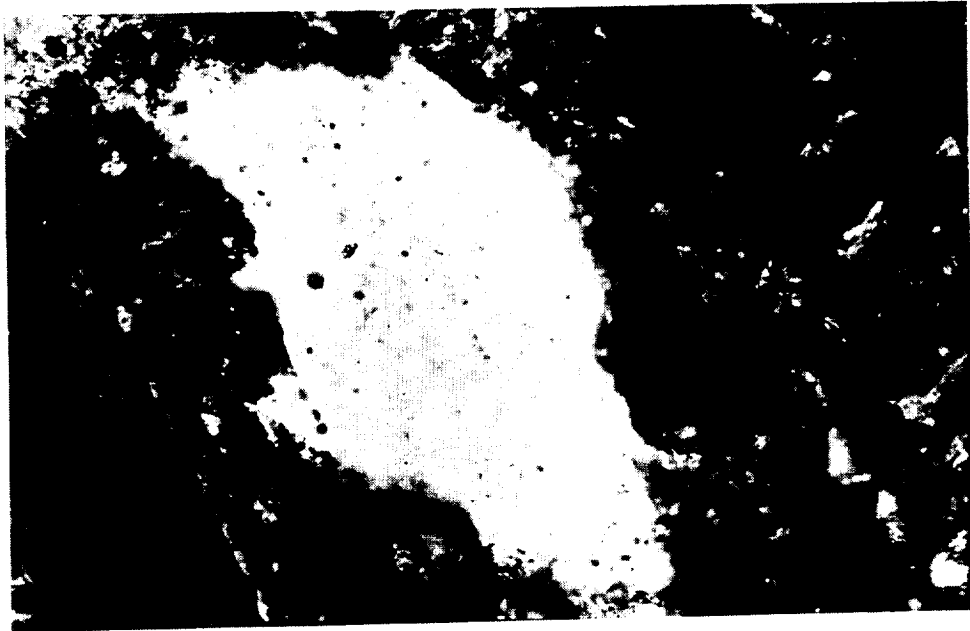
Plate II - Two quartz grains from core N10 of the Chicxulub No. 1 well showing northwest trending lamellae. Gunther Graup, personal communication.
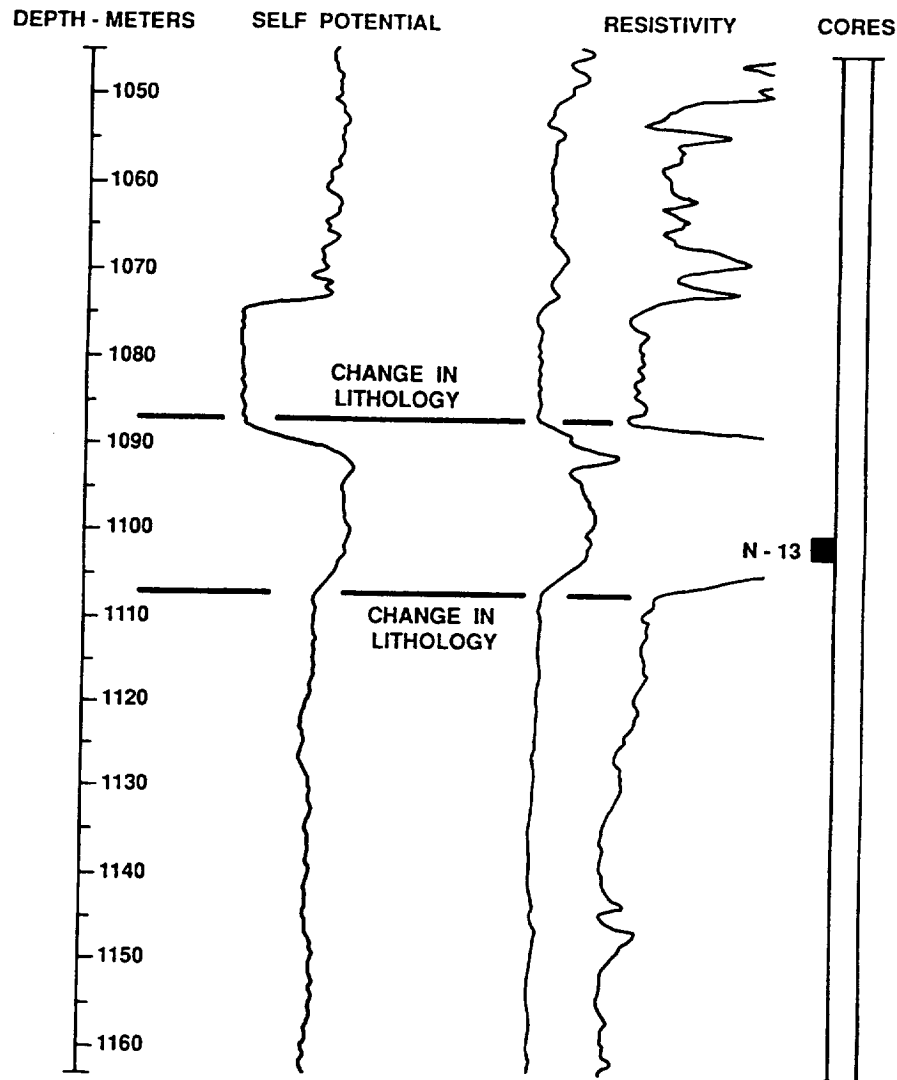
YUCATAN NO. 6 - ELECTRICAL LOGS

Figure 4. A portion of the electrical logs for the Yucatan No. 6 well. Note the change in lithology from 1087 to 1107 meter well depth. Arthur A. Meyerhoff, personal communication.

Further, Marin et al. have chosen to neglect two other cores which are pertinent to the biostratigraphy. Core N21 is at a depth of 1587-1590 m and core N22 at a depth of 1642-1645 m. Both are within the volcanic sequence. As stated previously, core N21 is described as limestone of Late Cretaceous age and core N22 as anhydrite and limestone of Turonian age.

In conclusion. Either the oil company geologists and paleontologists could not tell the difference between a limestone, sandstone, breccia, crystalline igneous rock, and anhydrite and could not distinguish between Turonian, Campanian, Maastrichtian, and Paleocene microfauna or the Chicxulub structure is a volcanic sequence of Late Cretaceous age. Isn't it time to ring down the curtain on this opéra bouffe and get on to other things?

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Common Patterns of Mass Extinction, Survival, and Recovery in Marine Environments: What Do They Tell Us About the Future?

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ABSTRACT

Mass extinction is characterized by the loss of more than 50 percent of the world's species within a short interval of geologic time - months to as much as 3 million years (My). In the fossil record, these events have primarily been recorded from the marine realm. Three patterns of mass extinction have been described - catastrophic, stepwise, and graded extinction. Many well-studied extinction intervals contain elements of more than one pattern, suggesting that these biotic crises were caused by varied forcing mechanisms linked by complex environmental feedback loops. This hypothesis is supported by the discovery that the four well-studied Phanerozoic mass extinctions (Late Devonian, middle and terminal Cretaceous, Eocene-Oligocene boundary extinctions) share a number of physical, chemical, and biological characteristics in common. They consistently show stepwise extinction patterns linked to intervals of extraordinary fluctuations in the temperature, chemistry and structure of ocean-climate systems, at rates and magnitudes well above background levels. In addition, tropical ecosystems were the first and most severely affected, and more poleward, temperate biotas were mainly stressed during the later phases of the extinction interval. Evidence for these unusual environmental changes is derived from high-resolution (cm-scale) paleobiological, sedimentological, trace-element and stable-isotope analyses spanning mass extinction intervals. These dramatic environmental fluctuations were the immediate causes of mass extinction, as they progressively exceeded the survival limits of global biotas largely adapted to warm, equable, ice-free climates which characterized over 90 percent of Phanerozoic time. These environmental fluctuations probably represented feedback phenomena from more powerful, short-term forcing mechanisms which abruptly perturbed the structure of ocean-climate systems. Multiple impacts of extraterrestrial objects within short (<1-3 My) time intervals - so-called meteorite/comet showers - are the most logical candidates. This hypothesis is supported by physical and chemical evidence for impacts clustered around most, but not all, Mesozoic and Cenozoic mass extinctions.

Mass extinction intervals broadly decimated life on Earth at least every 26-30 My for the post-Paleozoic, abruptly changing the structure of global ecosystems, altering the constraints of natural selection on evolutionary processes, and leaving large diverse areas of ecospace essentially barren and available to new evolutionary innovations. Whereas we now know enough about several mass extinction intervals to propose unifying hypotheses regarding rates, patterns and causes, we currently know almost nothing about the nature of life forms which survived mass extinction intervals, or about subsequent evolutionary

patterns and restructuring of ecosystems following these global biotic crises. Mass extinction intervals are commonly followed by some of the most rapid and innovative periods of evolutionary radiation in the history of the Earth. In order to be fully understood, mass extinctions must be studied from the standpoint of cause and effect, and should include detailed analysis of the extinction, the survival, and recovery intervals for each global biotic crisis.

Current theory would suggest that survivors of mass extinction are predominantly rare ecological and evolutionary generalists with broad adaptive ranges. But this hypothesis is difficult to defend in light of the rapid evolution, diversification, and restructuring of at least some major ecosystems following ancient mass extinction intervals. High-resolution stratigraphic investigations of the 0.25-0.5 My-long survival intervals following two Cretaceous mass extinctions demonstrate that, despite the scarcity of surviving fossil species, they represent diverse lineages, evolutionary grades, and adaptive strategies - exactly what would be expected from the nature of the ensuing evolutionary radiation. This, in turn, suggests a much broader range of survival strategies among the global biotas than previously suspected for mass extinction events. Seventeen such strategies have been identified, with well-documented examples. Surviving species fall into three categories: (a) Those that evolved during the high stress environments characteristic of the latest phases of mass extinction, and thus were adapted to these conditions (so-called Progenitor Species); (b) those that existed in small populations prior to the extinction event, but which subsequently underwent population blooms and biogeographic range expansion during the early survival interval (so-called Disaster Species); and (c) those that returned to a region from "hiding places" (refugia) where they had survived the extinction event (so-called Lazarus Species).

The recovery interval normally starts within 0.5 My of the last major extinction event and goes through two phases: (1) rapid evolution (radiation) of new species from surviving lineages, and (2) radiation of new species within new lineages, collectively leading to basic re-establishment of community structure and global ecosystems. But recovery time varies for different ecosystems, depending upon their ecological structure, complexity, and normal adaptive ranges. Temperate ecosystems characterized by low diversity communities regulated by physical and chemical factors of the environment seem to recover first, and most rapidly, after mass extinctions. Tropical ecosystems characterized by high diversity, equitable, complexly structured, biologically regulated communities recover last, sometimes millions of years after a mass extinction event. Reef ecosystems, for example, take 3 - 10 Ma to recover following ancient mass extinctions (Kauffman and Fagerstrom, 1993).

The data collected from the mass extinction events suggest that extinction-survival-recovery intervals are biologically very complex, yet broadly follow similar historical pathways. This allows the generation of unifying theory and development of predictive models that are applicable to understanding the short- and long-term effects of the modern biodiversity crisis. The rate of global change as a result of the activities of one species

(*Homo sapiens*), beginning 9-15 thousand years (Ky) ago and exponentially rising since the industrial revolution, is comparable to the most rapid environmental perturbation documented for any ancient mass extinction, including the terminal Cretaceous meteorite impacts. As a result of rapid deterioration in the Earth's environmental quality, and global loss or constriction of many natural habitats, decline in the diversity of life on Earth has also accelerated to levels that equate with the most rapid ancient mass extinctions. We may have lost over 50 percent of the global biodiversity in the last 15 ky, and especially in the last 200 years. This loss is at mass extinction levels, and the rate is increasing. Our Phanerozoic models predict that should this loss of diversity continue for another few centuries at current rates, mass extinction will reach such high levels, especially among tropical ecosystems, that recovery of the global ecosystem may again take millions of years.

INTRODUCTION

The evolution of Earth's biosphere has been repeatedly interrupted by great ecological crises - mass extinctions - which have resulted in mass killing, significant loss of global biomass, and the extinction of more than 50 percent of the world's species within geologically short time intervals (months to as much as 3 My: Kauffman. 1988a,b). The most famous of these extinctions eliminated the dinosaurs between 65.4 and 65.5 million years (My) ago. Mass extinctions are primarily reflected in the geologic record of organisms with well preserved hard parts. Whereas the disappearance of dinosaurs and other terrestrial organisms has captured the imagination of scientists and the general public, and symbolizes biotic catastrophe, the major evidence for rates, patterns and causes of mass extinction lies in the marine record.

Between 14 and 18 mass extinctions have been reported during the last 650 My of Earth history - Phanerozoic Time (Fig. 1). For the last 250 Ma, these mass extinctions have occurred at predictable intervals of 26-30 My (Raup and Sepkoski, 1984, 1986; Sepkoski, 1993) (Fig. 2), with one notable exception - the unparalleled extinction of life during the last 15 thousand years (Ky), and especially the last 200 years, associated with the global destruction of natural habitats by a single overpopulated species - Man, *Homo sapiens*.

Proposed causes for mass extinctions fall into two categories: (a) Those forcing mechanisms that reflect dynamic changes on planet Earth, for example: the effects of giant volcanic explosions; the escape of toxic gases and trace elements from cracks in the ocean floor, and their rise through the oceanic water column and into the atmosphere; widespread acid rain; rapid atmospheric and oceanic temperature changes; global greenhousing, or dense atmospheric dust and gas clouds; widespread loss of oxygen in the seas (global oceanic anoxic events, or OAE's); and rapid lowering of global sea level. Some of these phenomena, especially drops in sea level and oxygen depletion in the world's oceans, are commonly associated with, and may be partial causes for, mass extinctions (Hallam, 1984, 1989) . But, in general, no proposed Earth-bound forcing mechanisms statistically correlate with mass extinction events.

(b) Proposed extraterrestrial causes for mass extinction include: giant solar flares and nearby supernovae, both of which might greatly increase solar radiation to Earth; disruption of Earth's climate, and even its orbit, as a result of the gravitational attraction of close-passing field stars; passage of the solar system through the galactic plane (the Milky Way) every 30-33 My; large comet or meteorite impacts on Earth, and their consequent tectonic, oceanic, and atmospheric effects; and comet or meteorite showers, or storms (numerous impacts on Earth within a short time interval, predicted to be about 3 My; Hut et al., 1987). Of these, only meteorite and/or comet impacts, impact showers, and the effects of the galactic plane on the solar system during its periodic crossing are seriously considered as extraterrestrial causes for repetitive mass extinction events in Earth history. Intensive research on extraterrestrial impacts on Earth during the last 25 years have revealed that comets and meteorites have frequently hit our planet, at a predictable rate and in a spatially random manner that is compatible with impacting throughout the solar system (for example on our moon). These extraterrestrial events are now considered to be a predictable part of the evolution of life, and of Earth environments, through geological time.

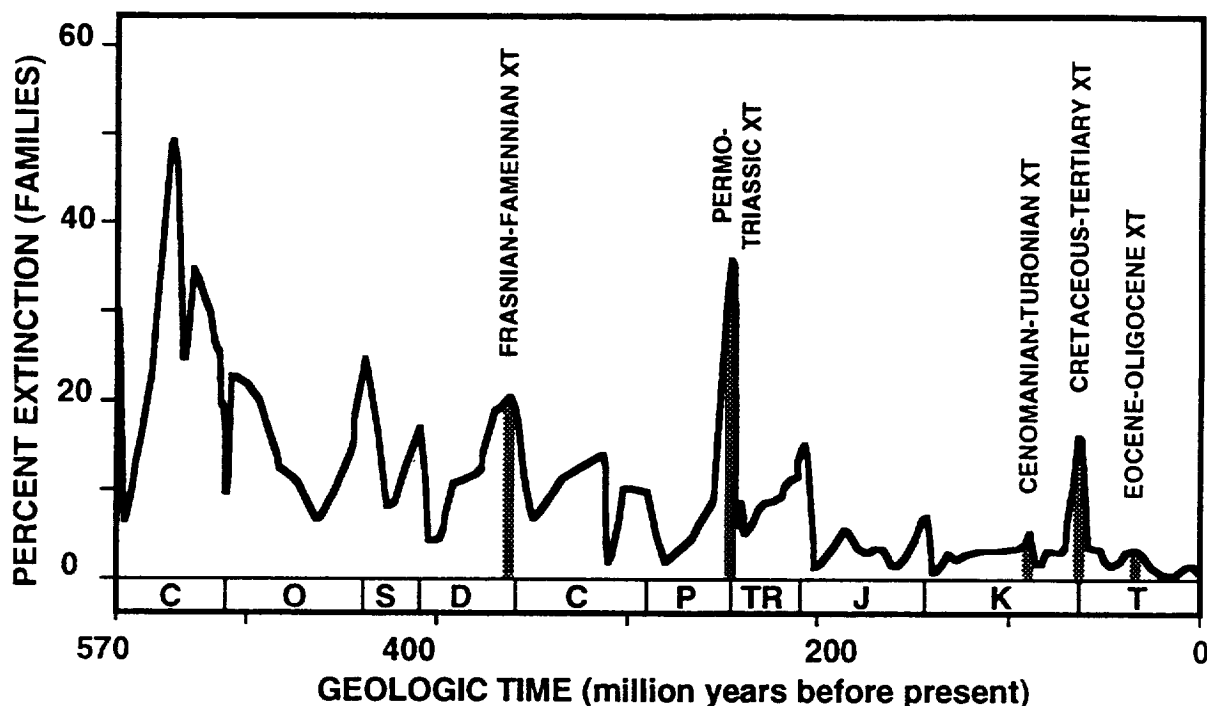TIME SERIES, PERCENTAGE OF FAMILIAL EXTINCTION (Modified from Sepkoski, 1993)

Figure 1 -- Graph showing the 18 Phanerozoic mass extinction peaks recorded as a time-series plot of family extinction (XT) percentages. Figure modified from Sepkoski (1993). Shaded vertical lines indicate well-studied mass extinctions discussed in this paper. Letters at bottom indicate geologic time periods: C = Cambrian; O = Ordovician; S = Silurian; D = Devonian; C = Carboniferous (Mississippian and Pennsylvanian); P = Permian; T = Triassic; J = Jurassic; K = Cretaceous; T = Tertiary.

Whereas mass extinctions have severely interrupted the diversification of life on Earth during its 3.5 billion years of recorded evolution, the global ecosystem has survived these crises and continued to expand through time (Fig. 3) (Sepkoski, 1993). This reflects the great resilience to extinction provided by high levels of genetic, ecological, and community diversity that existed prior to most mass extinction events. In general, the higher the global biological diversity just before a mass extinction interval, the more rapid the ensuing ecosystem recovery. Even mass extinctions associated with evidence for large meteorite or
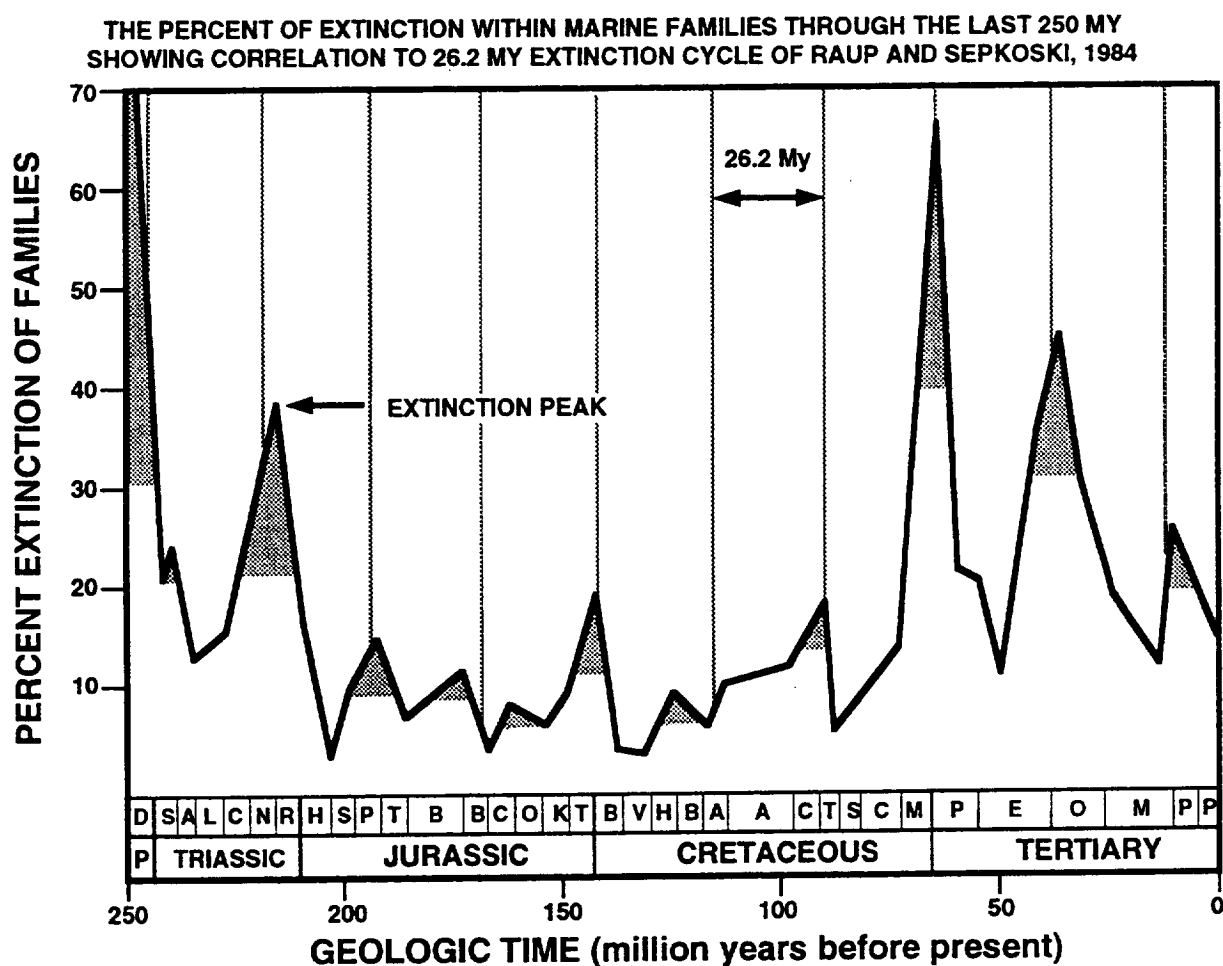
Figure 2 -- Graph showing the peaks of mass extinction (shaded) over the last 250 million years (My), based on analyses of marine families (modified from Raup and Sepkoski, 1984, 1986). These data statistically define a 26.2 My extinction cycle, represented by vertical lines. Although this cyclicity has been debated, mass extinction does appear to be non-random over the past 250 My, occurring every 26-30 My. Letters along bottom of diagram refer to stages within geologic periods.

comet impacts may show rapid recovery of basic ecosystems, usually within less than a million years, if pre-extinction biodiversity was high.

A similar relationship may exist between the "state of the global environment" (relative environmental stability or instability) associated with a mass extinction interval, the severity of the extinction event, and the rate of ecosystem recovery. The greatest of all extinctions, at the Permo-Triassic boundary (Teichert, 1990; Erwin, 1989, 1993), was also a time of severe long-term environmental decline characterized by continental aggregation to form the supercontinent Pangea, leading to aridity and large-scale temperature

DIVERSITY OF MARINE FAMILIES THROUGH TIME (Modified from Sepkoski, 1993)
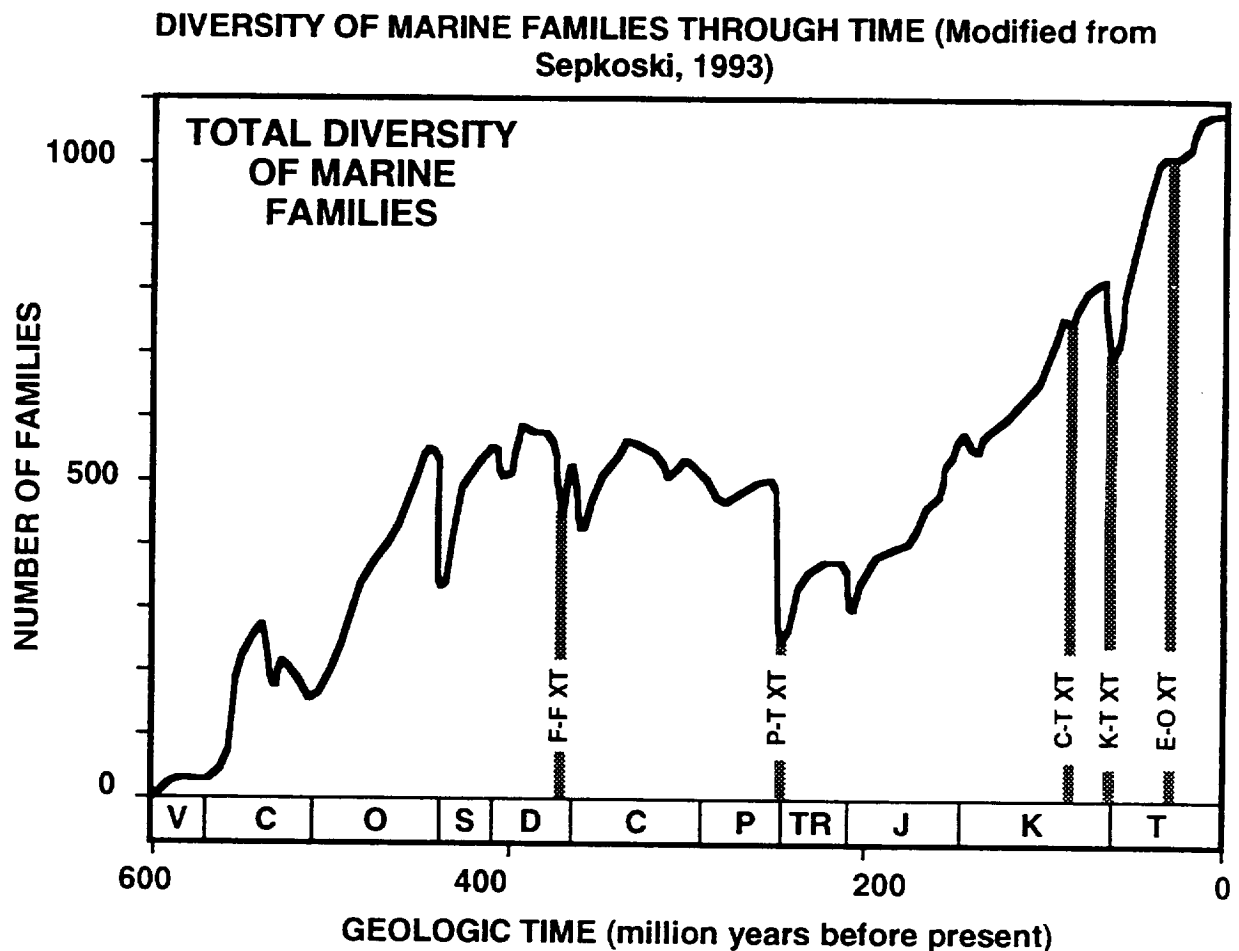
Figure 3 -- The record of diversity of marine families during the past 600 million years (modified from Sepkoski, 1993). Note overall increase in diversity through time. Dips in the curve represent mass extinctions. The most severe mass extinction events occur in the Cambrian (C); at the end of the Ordovician (O); in the Late Devonian (D); at the end of the Permian(P), and at the end of the Cretaceous (K); all of these have longer recovery times than the lesser extinctions. See Figure 1 for key to letters at bottom of diagram (Geologic periods), and to best-studied mass extinctions (shaded vertical lines), discussed in this paper.

variations in continental interiors, a major drop in global sea level and temperature, polar glaciation, and a general loss of prime ecospace world wide (especially in the Tropics). This, the greatest of all mass extinctions, was followed by a very long Triassic interval (10-20 My; Fig. 3) during which ecosystems very slowly recovered. In contrast, a Middle Cretaceous (Cenomanian-Turonian) mass extinction which occurred 93 My ago, during a time of high global sea level and warm equable climates (conditions thought to favor the diversification of life), was followed by nearly complete ecosystem recovery within less than a million years (Harries and Kauffman, 1990; Harries, 1993), except for tropical

MODELS FOR PATTERNS OF EXTINCTION
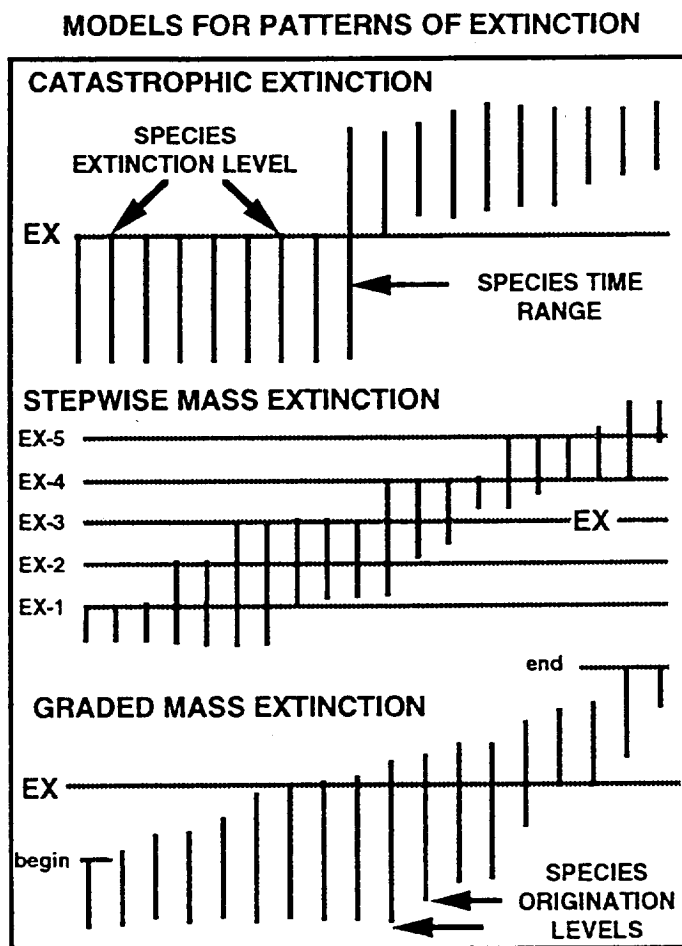
Figure 4 -- Models for the patterns of mass extinction observed in the fossil record (modified from Kauffman, 1988b). Catastrophic mass extinction modeled after the Cretaceous-Tertiary boundary associated with a giant meteorite impact (Fig. 8). Stepwise mass extinction modeled after the Late Devonian (Frasnian-Fammenian: Fig. 6), middle Cretaceous (Cenomanian-Turonian: Fig. 7) and Eocene-Oligocene (Fig. 9) mass extinctions. Graded mass extinction modeled after the Permo-Triassic extinction (Fig. 5), especially as viewed by Teichert (1990). Vertical lines on figure schematically reflect the time ranges of major groups of organisms.

ecosystems (Kauffman and Fagerstrom, 1993). This paper is abstracted from a more comprehensive review to be published, in Spanish, by the Museu de la Ciencia de la Fundacio "La Caixa" in Barcelona, Spain (Kauffman, 1994a, in press).

PATTERNS OF MASS EXTINCTION

The long-term effects of mass extinction phenomena on global biodiversity may also be regulated by the patterns of extinction. Among a complex spectrum of extinction fabrics and their many causes, three basic patterns emerge (Kauffman, 1988) (Fig. 4).

CATASTROPHIC MASS EXTINCTIONS (Fig. 4), interpreted as taking only days to hundreds of years, are related to extraordinary short-term perturbations of the global environment, for example giant meteorite or comet impacts. Such catastrophes simultaneously affect genetically and ecologically diverse taxa, and most global

GRADED EXTINCTION ACROSS THE PERMO-TRIASSIC BOUNDARY
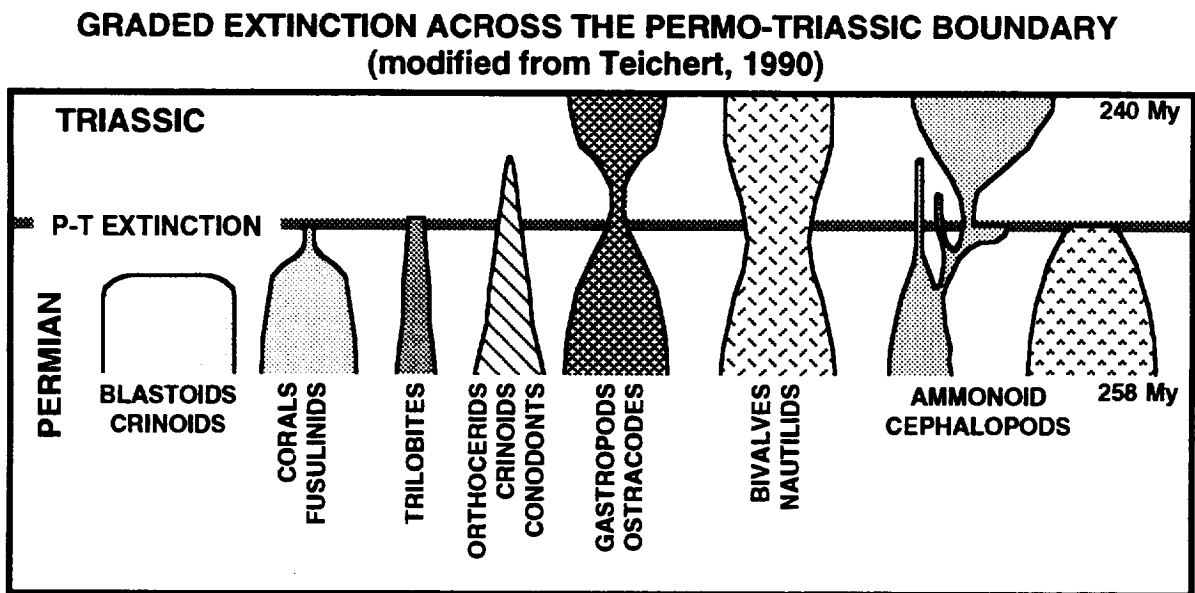### (modified from Teichert, 1990)

Figure 5 -- Graded mass extinction as represented by patterned graphs showing the time range (height) and diversity (width) of major groups of organisms across the Permo-Triassic extinction boundary (modified from Teichert, 1990). Note early, abrupt extinction of reef-building corals and associated crinoids and blastoids, and more graded (tapered) extinction patterns of predominantly temperate molluscs, trilobites, crinoids, conodonts and ostracodes. The entire extinction interval lasts 8-10 My; Erwin (1993), however, documents a shorter, more dramatic extinction interval within 1-2 My of the Permo-Triassic boundary.

ecosystems, regardless of their location or inherent survival "strategies." The predictions of catastrophic mass extinction are that survivors will be few, predominantly ecological generalists (Jablonski, 1986) and refugia species, and that recovery will be very long-term, spanning millions of years. The great Cretaceous-Tertiary (K-T) mass extinction, associated with evidence for at least one and probably several closely spaced meteorite and/or comet impacts (McHone and Dietz, 1991), comprises the main example of a global biological catastrophe (Alvarez et al., 1980, 1984). Yet, as we shall subsequently see, the patterns of K-T extinction are complex, spread out over 2-3 My, and recovery is faster than predicted in both terrestrial and marine ecosystems (Kauffman, 1988b) (Fig. 8). There may have been no mass extinction catastrophes on Earth related exclusively to a single large impacting event, despite this common assumption for the end of the age of dinosaurs. The ecological resilience of life argues against this as long as biodiversity is high.

STEPWISE MASS EXTINCTIONS (Fig. 4) involve a series of closely spaced, short-term (<100 Ky), ecologically selective extinction events. These are generally spaced 100 to 500 Ky apart; collectively, stepwise extinction events are spread over 1-3 My intervals. Between these steps, extinction rates return to background levels, and both origination of new species and initial ecosystem recovery may occur (Kauffman, 1988b). In well-studied Devonian and Cretaceous examples, tropical and subtropical organisms are most affected during early steps of extinction, and ecologically more resilient temperate and poleward groups are most affected during later steps (Kauffman, 1979, 1988b). Successive steps within a single mass extinction interval are commonly associated with physical and geochemical evidence for rapid, large-scale changes in ocean-climate systems (e.g., Fig. 7), and in some cases, with evidence for one or more comet or meteorite impacts. Comet and/or meteorite showers may be the initial catalyst for these ocean/climate perturbations, which then perpetuate over longer periods through complex environmental feedback processes (Kauffman, 1988b; 1994b in press). The well-studied Cenomanian-Turonian (middle Cretaceous) mass extinction (Fig. 7) is an outstanding example of a stepwise mass extinction (Elder, 1989; Kauffman, 1988a,b, 1994b).

GRADED MASS EXTINCTIONS (Fig. 4) refer to intervals of 1->5 My during which rates and/or magnitude of extinction exceeds origination of new species to create >50 percent reduction in species diversity. Yet, the pattern of species loss is similar to, but more accelerated than, background extinction. Causal mechanisms for graded mass extinction are generally regarded as Earth-bound, including persistent sea-level fall, oceanic oxygen depletion, chemical poisoning, prolonged intervals of temperature change, etc. In examples like the Permo-Triassic mass extinction (Fig. 5: Teichert, 1990; Erwin 1993), there is again ecological gradation through time in loss of taxa and ecosystems, from more tropical or equatorial, to more temperate and polar forms.

CHARACTERISTICS OF WELL-STUDIED MASS EXTINCTION INTERVALS

To date, of the 14 - 18 recorded Phanerozoic mass extinctions, only four have been intensely studied through high-resolution (cm-scale) stratigraphic analysis of interdisciplinary data sets which span not only the mass extinction event(s), but also post-extinction history. These are: (a) The Upper Devonian Frasnian-Famennian (F-F) mass extinction, 380 My ago; (b) the middle Cretaceous Cenomanian-Turonian (C-T) mass extinction, 93.4 My ago; (c) the Cretaceous-Tertiary (K-T) mass extinction, 65.4 My ago, marking the end of the age of dinosaurs; and (d) the Eocene-Oligocene (E-O) mass extinction, 36.3 My ago (Figs. 1,2). Many other mass extinctions are currently receiving detailed study, for example those at the Precambrian-Cambrian boundary, the Late Ordovician, the Permo-Triassic boundary (the greatest extinction of all Earth history), the Triassic-Jurassic boundary, and the Late Miocene. The basic characteristics of these four well-known mass extinctions are summarized below; Figures 6-9 show characteristic data from these mass extinctions:

(a) FRASNIAN-FAMENNIAN (F-F: LATE DEVONIAN) MASS EXTINCTION (Fig. 6): This extinction interval spans about 2.2 My (Walliser et al., 1988, 1989; Schindler, 1990). Global sea level was high, climates warm and equable. There are five discrete steps of extinction among: (a: first) styliolinid conodont taxa; (b) tropical coral-stromatoporoid reefs; (c) cephalopod and trilobite families; (d) gephuroceratid cephalopods, homoctenids, and entomozoids; and (e; finally) extinction of the last homoctenids (Schindler, 1990). Two major oceanic oxygen-depletion events, represented by two laminated black shale intervals (the lower and upper Kellwasser horizons; Fig. 6), are associated with abrupt, large-scale geochemical fluctuations in stable isotopes, organic carbon, and trace elements, depicting environmental chaos in ocean-climate systems. In China and Canada, a trace-element enrichment layer, including Iridium, has been recorded at the Frasnian-Famennian extinction boundary, suggesting at least one meteorite/ comet impact on Earth (McLaren, 1989; Wang et al., 1991).

(b) CENOMANIAN-TURONIAN (C-T: MIDDLE CRETACEOUS) MASS EXTINCTION (Fig. 7): This global extinction spans 1.5 My and occurred during a major global greenhouse interval (CO_2=>3X modern levels; Berner, 1994), warm equable climates, very high global sea level (>300 m above present sea level), and widespread oceanic oxygen-depletion (the Bonarelli Oceanic Anoxic Event). It is associated with short-term, large-scale, geochemical fluctuations (13^C, 18°, organic carbon; Kauffman, 1988a,b; 1994b) (Fig. 7), reflecting rapid variations in oxygen levels, carbon cycling, temperature and/or salinity in the world's oceans and seas - conditions that would exceed the survival limits of organisms adapted to relatively stable warm Cretaceous oceans. Numerous trace element enrichment levels (including three Iridium peaks) are associated with the early, most severe part of this extinction interval (Orth, et al., 1988, 1993), possibly marking abrupt overturn of oceanic waters and upward migration of toxic trace metals through the water column. Possible causes are (a) remobilization of trace elements from oceanic sediments during touch-down of oxygen-depleted water masses; (b)

FRASNIAN-FAMENNIAN STEPWISE MASS EXTINCTION: DATA FROM STEINBRUCH SCHMIDT, GERMANY (Modified after Schindler, 1990)
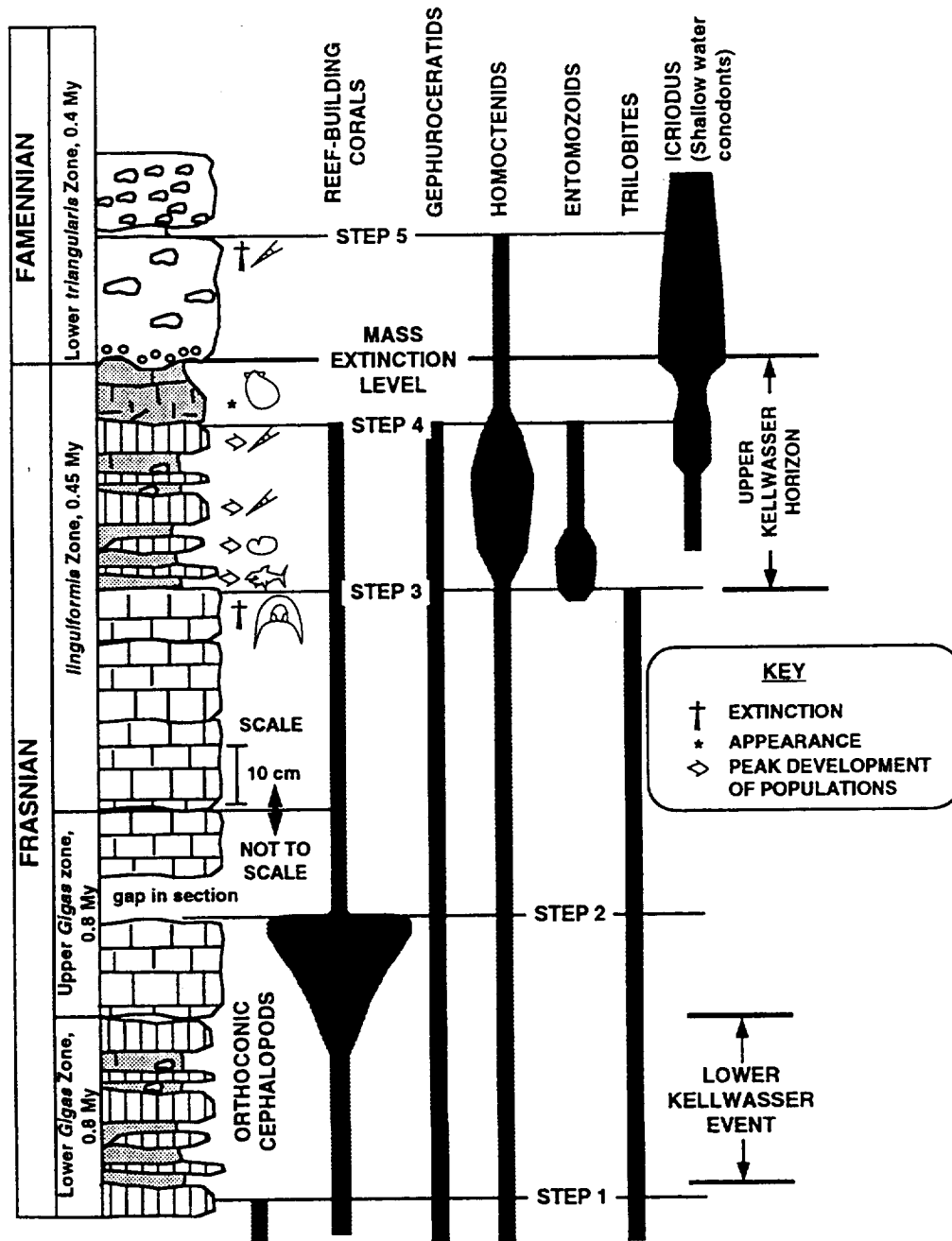

Figure 6 -- Stepwise mass extinction patterns across the Late Devonian, Frasnian-Famennian stage boundary, as shown by data from the Harz Mountains of Germany (modified from Schindler, 1990). Vertical dark lines show time ranges of major marine groups, labeled at top; expansions in these lines denote times of maximum species diversity and abundance. Lower and Upper Kellwasser events are dark shale intervals representing widespread oxygen depletion in world oceans.
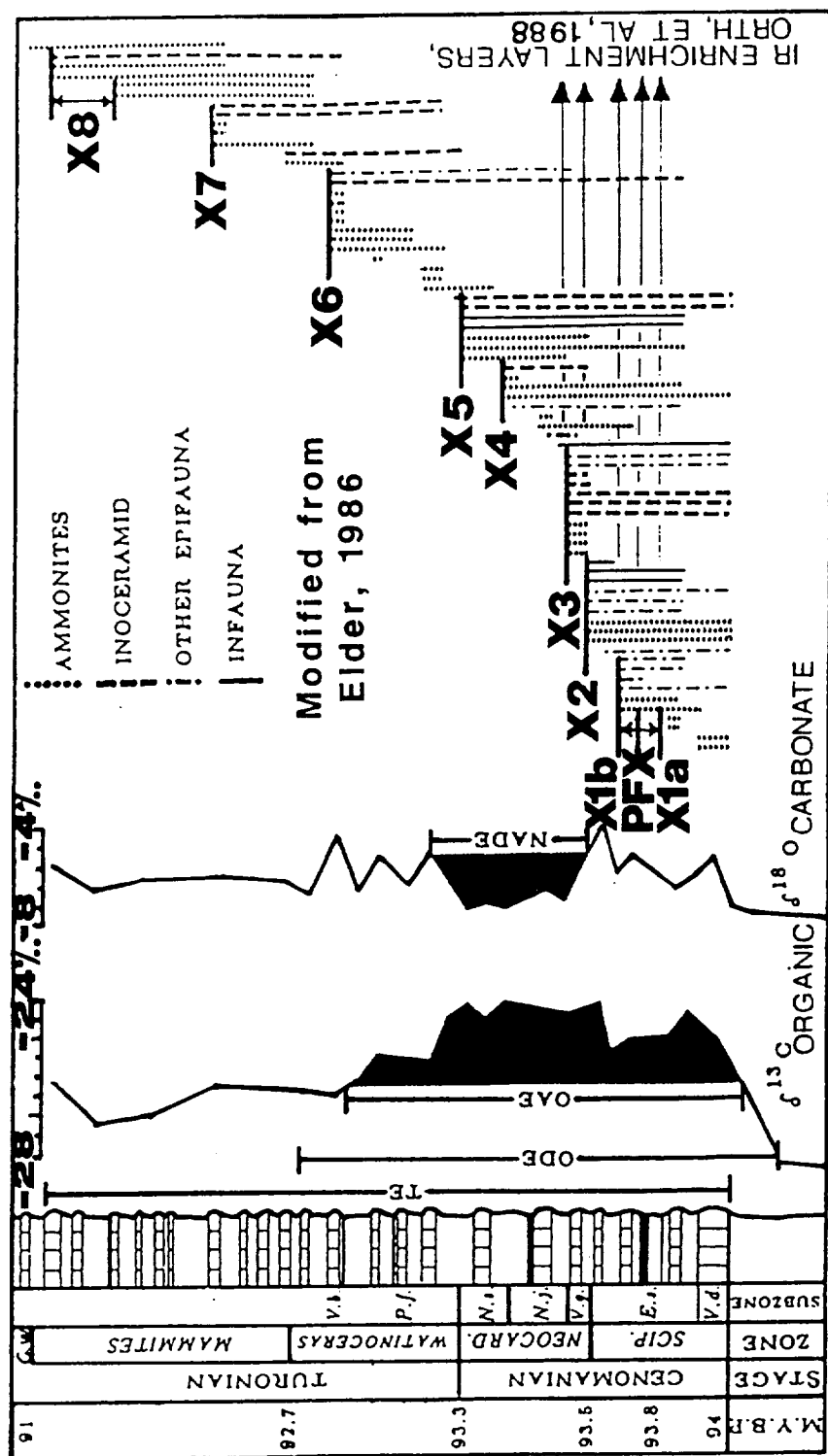
Figure 7 -- Stepwise patterns of molluscan species extinction across the Cenomanian-Turonian (mid-Cretaceous) boundary mass extinction interval. Data are compiled from sections in the Western Interior Basin of North America (after Elder, 1988; Kauffman, 1988b; Harries and Kauffman, 1990). Vertical lines depict known species ranges; key to line patterns at top of diagram. Extinction steps are designated X1-X8, all of which are later than the earliest C-T extinction event of Caribbean reefs (Johnson and Kauffman, 1990). PFX = extinction level of keeled, rotaliporid planktonic foraminifera. Arrows to right of horizontal lines show levels of unusual trace element enrichment in sediments, including Iridium (Ir) (impact signals?), which correlate precisely with the first five extinction steps. Note major interval of unusually large-scale fluctuations in stable isotopes (^{13}C, ^{18}O), defining major perturbations in carbon cycling, salinity (NADE) and/or temperature, and an oceanic anoxic event (OAE); these collectively describe an oceanic destabilization event (ODE) which spans the entire mass extinction interval. This is the best documented example of stepwise extinction.

comet/meteorite impacts in the ocean; and (c) seafloor outgassing during a major re-arrangement of the Earth's plates and peak development of the Pacific superplume, a rising mass of molton magma resulting in widespread volcanism (Larson, et al., 1991a,b). Marine extinction levels reached 25-30 % of microplankton species, and 50-76 % of marine molluscan species (clams, snails, cephalopods) (Elder, 1989). The terrestrial record is still poorly known. Extinction began 0.5-1 My below the C-T boundary with the demise of tropical reef ecosystems (Johnson and Kauffman, 1990), and proceeded through seven additional steps into the Early Turonian (Fig. 7; Kauffman, 1988a,b; 1994b; Elder, 1989). Steps 2-4 (Late Cenomanian) were the most severe, involving successive loss of tropical microplankton and molluscs (mainly ammonites), warm-water to cosmopolitan molluscs, and finally (steps 5-7) more temperate invertebrates. These extinction steps are encompassed within the interval of large-scale geochemical fluctuations. The first five extinction steps are precisly correlative with Iridium and other trace metal enrichment peaks and stable isotope fluctuations, suggesting a cause-effect relationship between impacting and oceanic mixing (Fig. 7; Kauffman, 1988b; 1994b). Three to five Iridium enrichment levels suggest an impact shower, an hypothesis supported by the association of two extinctions and trace element enrichment levels with impact debris (shocked quartz or microtektites). Three major terrestrial impact craters are dated 1-6 My prior to the first C-T extinction step (Grieve, 1982). These data support the hypothesis that a meteorite/comet shower was the initial catalyst for major ocean/climate destabilization, expressed as dynamic thermal and chemical feedback processes.

(c) CRETACEOUS-TERTIARY (K-T) MASS EXTINCTION (Fig. 8): This is the most famous and one of the most thoroughly studied mass extinctions, and marks the end of the age of Dinosaurs. It is the one for which a terrestrial impact is most clearly associated with mass extinction. The largest known impact crater on Earth (Chicxulub Crater, Yucatan Penninsula, Mexico) has an age of 65-66 My (K-T boundary; Smit et al., 1992); as many as 11 terrestrial impact craters are known within a 3-4 My interval spanning the K-T extinction boundary (McHone and Dietz, 1991). Sedimentary evidence for a K-T boundary impact includes shocked quartz, microtektites, and a boundary clay (fallout of fine impact debris). The K-T mass extinction occurred during falling global sealevel, oxygenated oceans, cooling global temperatures, and declining atmospheric CO_2 (<2X modern levels; Berner, 1994). Geochemical analyses show rapid, large-scale fluctuations in oceanic chemistry and temperature across the K-T boundary, depicting destabilization of global ocean-climate systems. Trace metals, including Iridium, are enriched at and just below the K-T boundary, correlative to large meteoritic impact(s) (Alvarez et al., 1980, 1984). The K-T extinction follows a stepwise pattern (Fig. 8; Kauffman, 1988b), with the largest extinction step (a global catastrophe) at the K-T boundary associated with impact-related environmental disruption. Extinction initiates 1-1.5 My below the K-T boundary with abrupt destruction of reef communities and mass killing within all tropical marine ecosystems (Johnson and Kauffman, 1990), and proceeds through three additional steps to the K-T boundary (Fig. 8): (a) extinction among warm-temperate and cosmopolitan molluscs, and possibly reptiles, 0.5 Ma below the boundary; (b) a first shock to the oceanic plankton, and loss of many specialized tropical-subtropical groups, within 100 Ky
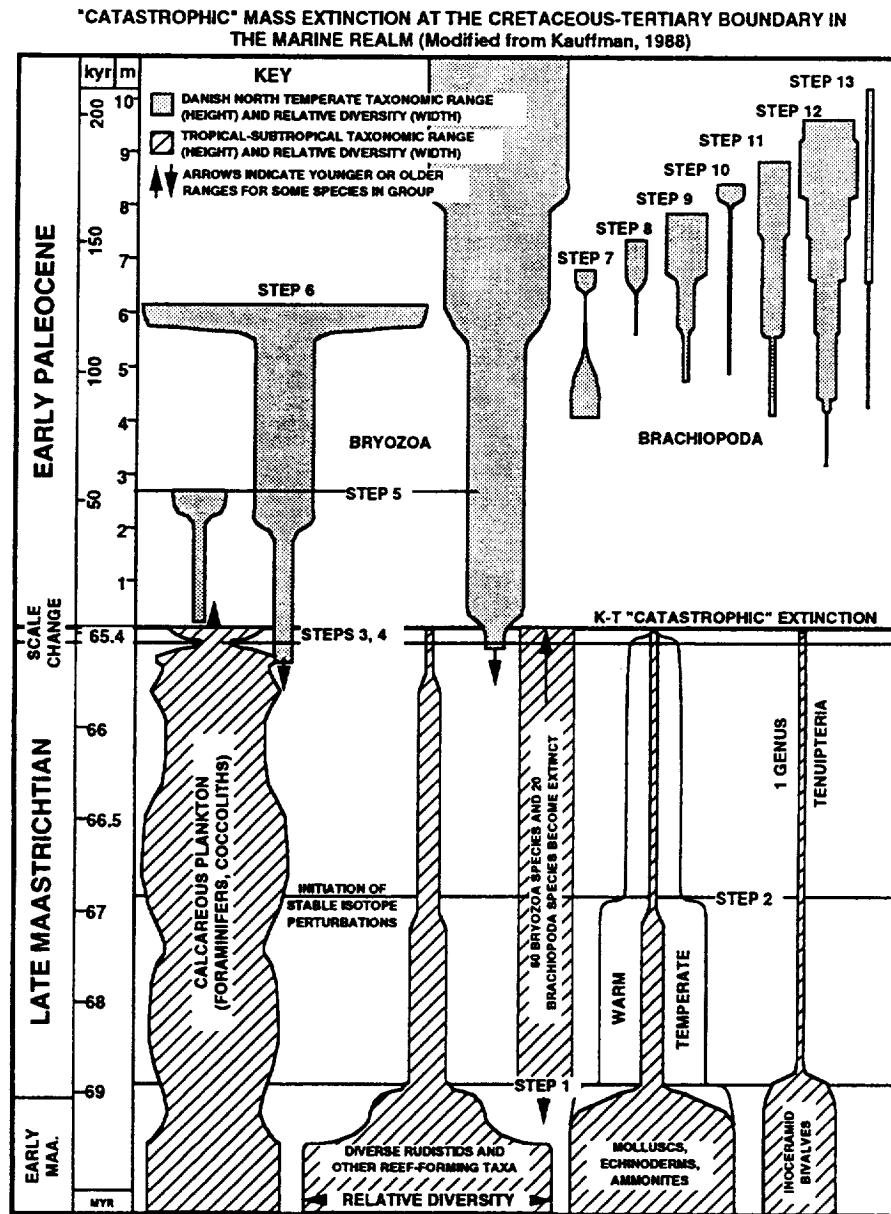
Figure 8 -- Generalized marine data for the Cretaceous-Tertiary (K-T) mass extinction interval. Vertical lines show time ranges of major groups of marine organisms which became extinct around the boundary, with the width of these lines indicating relative diversity within each group, but not to scale (modified from Kauffman, 1988b). The mass extinction interval spans 3-4 My, even though at least one large meteorite impact at the K-T boundary was directly and indirectly responsible for a large proportion of the mass extinction. These extinction steps, beginning with demise of the tropical reef ecosystems about 1.5 My below the boundary and ending with extinction among north temperate taxa in the basal Paleocene (Tertiary), are associated with trace element and stable isotope perturbations, as well as evidence for multiple impacting events, spanning much of the mass extinction interval.

of the boundary; and (c) the "catastrophic" portion of the extinction, associated with K-T impact, resulting in 75 to >90 percent loss of oceanic plankton species, the final extinction of many typical Cretaceous marine organisms, the disappearance of dinosaurs, and loss of >65 % of the terrestrial plant species (Wolfe and Upchurch, 1986). Extinction steps continued into the Paleocene among north-Temperate invertebrates for another 250 Ky (Fig. 8: early recovery interval: Kauffman, 1988b).

(d) EOCENE-OLIGOCENE (E-O) MASS EXTINCTION (Fig. 9): The E-O extinction spanned 3-4 My (Middle-Late Eocene) with major fluctuations in temperature, ocean chemistry, and falling, but fluctuating sea level; at least 3 impact events are represented by microtektite horizons (Keller, 1986; Kauffman, 1988b); one Iridium enrichment layer, and at least one associated terrestrial crater. Each extinction step is abrupt, spaced about 1 My apart, and is associated with loss of 25 - 52 % of extant calcareous plankton living at that time. The youngest three steps are associated with major North American molluscan extinctions: 63-89 %of bivalves (clams), and 72 to 97 % of gastropods (snails) (T. Hansen in Hut et al., 1987; Kauffman, 1988b). Origination of new species exceeded loss between extinction steps; overall, plankton and mollusk diversity decreased through the interval. The E-O mass extinction is contained within a zone of rapid, large-scale geochemical fluctuations indicating disruption of global ocean-climate systems.

A UNIFYING HYPOTHESIS FOR MASS EXTINCTION

These four mass extinctions share a number of characteristics, some of which are also now known for other mass extinction intervals. These shared are: (a) all show a stepwise pattern of extinction; statistical tests of the stepwise pattern are not yet completed. The stepwise extinctions in three examples are ecologically graded through time from more tropical to more temperate ecosystems; (b) all four mass extinctions span a 1.5-4 My interval, and are not catastrophic; (c) each extinction is bracketed by unusually rapid, large-scale geochemical fluctuations, as depicted in stable isotope, organic carbon, and trace-element analyses; these depict extraordinary, short-term, large-scale disturbances in ocean-climate systems, the initiation of which is coincident with early extinction steps; and (d) each extinction is associated with direct physical and chemical evidence for one or more meteorite and/or comet impacts on Earth; these data mostly reflect terrestrial and very shallow water collisions. Oceanic impacts do not necessarily produce significant physical evidence (e.g. craters, impact ejecta), but even small impactors will cause tremendous oceanic stirring, resulting.in rapid changes in temperature, chemistry, circulation and stratification of ancient oceans. Because only 20-25 % of the Earth's surface lay above water during these times, and impacting is stochastic and spatially random, the total number of impacts during these extinction intervals is thought to be four- to five-times greater than those for which we actually have physical evidence from terrestrial craters, impact fallout debris, and microtektites. This suggests that marine geochemical perturbations and trace-element enrichment levels may provide important new evidence for comet or meteorite showers/events linked to mass extinctions.

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SUMMARY OF EOCENE-OLIGOCENE EXTINCTION EVENTS (SOURCE: G. Keller and T. Hansen in Hut et al., 1986; modified from Kauffman, 1988)
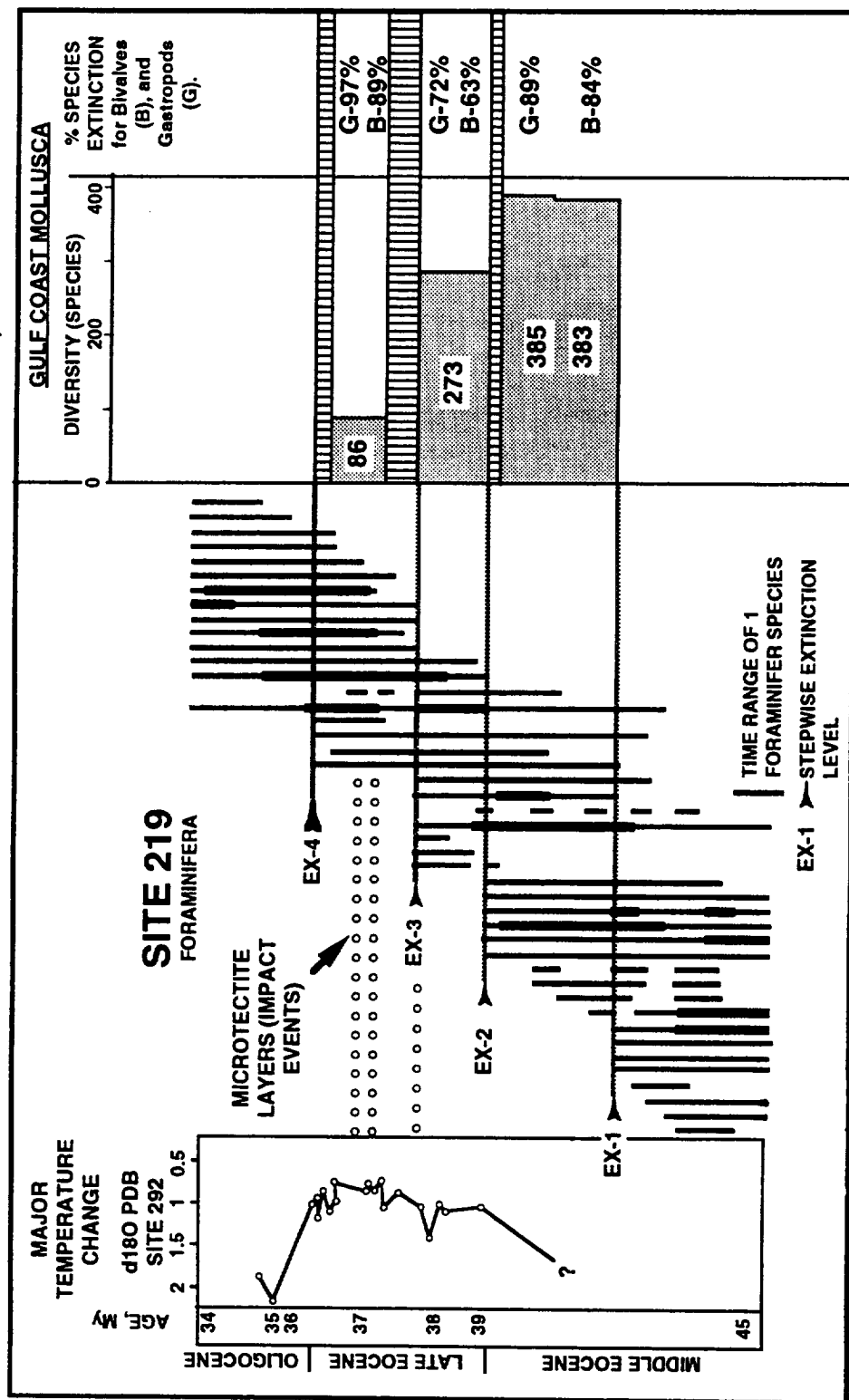
Figure 9 -- Compilation of biological and geochemical data across the Eocene-Oligocene mass extinction interval, showing: (a) stepwise extinction pattern among planktonic foraminifera from the Deep Sea Drilling Program site 219: extinction steps are labeled EX-1 - EX-4; (b) steps of Gulf Coast Eocene molluscan extinction, showing diversity reduction among bivalve (B) and gastropod (G) species; (c) three levels of micro-tektites - rapidly cooled spherules of impact melt rock, represented by horizontal lines of small circles; and (d) stable isotope (^{18}O) data showing a major temperature change (cooling) across the E-O boundary. (modified after Kauffman, 1988b, based on data of Keller and Hansen in Hut et al., 1987).

These shared characteristics for the best known mass extinctions, and some still under study, permit a comprehensive hypothesis of mass extinction to be developed and subsequently tested. The main elements of this hypothesis are as follows:

(1) For much of life history, tropical to warm-temperate climate zones were greatly expanded, and warmer, more equable ocean-climate systems prevailed than occur today (a glacial interval). Organisms evolving over millions of years within these equable climate/ocean systems probably had narrower environmental tolerances (adaptive ranges) than those of today, and were most similar to living tropical species. During most of geologic time, organisms, ecosystems, and ocean-climate systems were more delicately perched, with narrower environmental thresholds, than modern analogues; they were more susceptible to perturbation and extinction than today. Even small, rapid changes in key environmental factors, e.g. due to oceanic impact, might have produced widespread ecosystem shock and a series of negative feedback processes that initiated and perpetuated mass extinction.

(2) The most likely candidate for the abrupt global or regional changes in environmental systems we record in the geochemical and paleontological records of mass extinction is extraterrestrial impacting, especially in the world's oceans. A single impactor less than 1 kilometer in diameter would cut through Earth's atmosphere and oceans, and impact on the ocean floor, within seconds. Such an event would cause far-reaching shock waves, compaction and rapid heating of the nearby water column, disruption and mass movement of oceanic sediments, tsunamis (giant tidal waves), and would completely mix and disrupt the oceanic water column at least within the target basin. This would, in turn, cause rapid mixing of benthic sediments and ocean water, overturn and advection of oxygen-depleted watermasses rich in potentially toxic trace elements, and eventually far-reaching fluctuations in ocean temperature and chemistry through a series of longer-term environmental feedback loops that would continue to stress global ecosystems for hundreds to thousands of years. These rapid, large-scale chemical and thermal perturbations, represented by abrupt trace element, carbon and stable isotope fluctuations, are the most likely killers of marine organisms during global biotic crises. Terrestrial impacts could act even more severely, but for shorter periods of time, through flash fires, the development of high-altitude clouds of impact debris, smoke, and water vapor, reduction of solar radiation, rapid global cooling, and subsequently, acid rain. Even the dinosaurs could not survive under these conditions.

(3) In support of this hypothesis is the association of physical and chemical evidence of one or more, land-based, meteorite or comet impacts with all four well-studied Phanerozoic mass extinctions: multiple impacts occurred during or just before three of the four extinctions; these reflect impact showers clustered around 30 My intervals (Alvarez and Muller, 1984; Hut et al., 1987). If our physical and chemical record of impact showers around the C-T, K-T, and E-O mass extinctions is largely drawn from terrestrial and shallow-water target sites, if impacting on Earth is stochastic and spatially random, and if the Earth was 75-80 percent covered with water during much of Earth history due to

higher global sea level, then it is probable that for every impact event that we can physically detect in the rock record, there were at least four or five additional oceanic impacts that we have not detected by conventional means. For temporally clustered impact craters within 3-4 My intervals, this relationship suggests major comet/meteorite showers of 15 (C-T) to 55 (K-T) events. These observations collectively support the concept that comet and/or meteorite showers were commonly associated with mass extinctions, with the majority of impacts (and probably the earliest ones) landing in the world's oceans, where they would be catalysts for the abrupt, large-scale shifts in temperature, chemistry, and carbon cycling documented for well-studied mass extinctions. These geochemical fluctuations are commonly associated with individual extinction events (steps), and are interpreted as being the main killing mechanisms for marine organisms adapted to a predominantly warm, equable Phanerozoic world.

(4) Thus, based on the close correlation of both direct and indirect evidence for impact showers, abrupt, large-scale ocean/climate perturbations, and discrete mass extinction events (steps) for many, and possibly most, Phanerozoic biotic crises, a multicausal hypothesis for mass extinction emerges. Against a backdrop of episodic, low density impacting on Earth, periodic comet (most likely) and meteorite showers occurred about every 30 My, probably due initially to perturbations of the Oort Comet Cloud that surrounds the solar system. Proposed causes for these perturbations range from random passing field stars, to a solar companion star, to passage through the galactic plane. Once initiated, there would be a dramatic increase in the number of Earth-crossing and impacting comets and possibly meteorites. After the initial perturbation, impacting would then gradually return to background levels over a 3 My interval, as modeled by Hut et al. (1987). This is, interestingly, the average duration of well-studied stepwise mass extinction intervals. The result of a comet/meteorite shower would thus be a series of closely spaced impacts on Earth over a period of 1->3 My, 75-80 percent of which would land in the world's oceans. This hypothesis would therefore predict 5 (Late Devonian) to 55 (Cretaceous-Tertiary boundary) impacts in showers associated with well-studied mass extinction intervals. These projected totals are based on the number of known terrestrial impacts associated with each extinction event, the spatially random nature of impacting, and the amount of Earth covered by water at these times. There is a high probability that the earliest and the majority of impacts in a shower would be in the sea and would initiate a series of exceptional physical, chemical, and thermal perturbations of the ocean/climate system, geochemically represented by the extraordinary carbon, stable isotope, and trace-element fluctuations which commonly envelope well-studied mass extinctions in the stratigraphic record. These events would continue to perturb oceanic environments well after impact through dynamic feedback processes; the exceptional rate and magnitude of these repeated ocean-climate perturbations would be the primary causes for stepwise extinction of tropical (first) through successively more temperate, broadly adapted ecosystems with repeated exposure to high-stress events. This extinction mechanism would be especially effective when acting on a global biota that was narrowly adapted to the relatively stable, warm, greenhouse environments that characterized much of the Phanerozoic. The length of each mass extinction interval would reflect the duration of the

meteorite/comet shower, plus the duration of the last impact-generated environmental feedback loop, before restabilization of the global environment. Larger-scale extinction catastrophes, as at the Cretaceous-Tertiary boundary, reflect rare impacts of exceptionally large objects (5->10 km in diameter), such as that creating the Chicxulub Crater in Mexico, the largest known impact structure on Earth.

This hypothesis views mass extinction as a complex, multicausal phenomenon in which meteorite and/or comet impacting acts as a catalyst for dynamic feedback responses in ocean-atmosphere systems. These in turn, stress global biotas along a broad ecological gradient to create a biological crisis. This hypothesis best fits the most highly resolved data for the four well-studied mass extinctions. The hypothesis potentially has predictive power, both in the nature of biological response to various types of stresses during mass extinction, but also in the way in which a mass extinction evolves over short and long time intervals. Based on this model, for instance, we seem today to be in the first stages of a mass extinction, with exceptionally rapid, large-scale loss of species in tropical ecosystems (rain forests, reefs) which may soon reach 50 percent of the calculated tropical species diversity.

THE AFTERMATH OF MASS EXTINCTION; SURVIVAL AND RECOVERY INTERVALS

In spite of the progress made in documenting the basic patterns and diverse causes for ancient mass extinctions, and in constructing a testable extinction hypothesis, the aftermath of mass extinction is poorly understood. Extinction is only the first of three phases in the biological history of a mass extinction interval (Harries and Kauffman, 1990; Harries 1993); it is followed by a *survival interval* characterized by population expansion among pre-extinction species which were able to maintain at least small viable populations through the extinction interval. This, in turn, is followed by a *recovery interval* during which both new and surviving lineages undergo evolutionary diversification leading to re-establishment of basic ecosystems (Fig. 11). Collectively, these two phases rarely exceed one million years in duration for all except the most severe mass extinction events, or in the case of tropical ecosystems (e.g., reefs) which may take 4 - 10 My to restructure after a mass extinction (Kauffman and Fagerstrom, 1993). The detailed documentation and interpretation of survival and recovery intervals following a mass extinction is critical to understanding the whole spectrum of dynamic changes associated with the mass extinction process.

The SURVIVAL INTERVAL follows the last major step in ancient mass extinctions and is very poorly fossiliferous in most examples. It represents a relatively short period of time, usually less than 250 thousand years (Harries and Kauffman, 1990; Harries 1993). The paucity of fossils seems to support the hypothesis (Jablonski, 1986) that mass extinction widely decimates ecologically and genetically diverse groups, irregardless of their normal survival strategies, and that only the most broadly adapted forms (ecological generalists) survive extinction-related environmental stresses.

But in contradiction to this theory, the rate of biological diversification and basic ecosystem recovery following well-studied mass extinctions is remarkably fast for all but tropical (e.g., reef-related) communities, usually taking place within the first one-million years. This is too fast to expect from even the most rapid evolutionary changes among a few broadly adapted (eurytopic) lineages, groups that have generally been shown to evolve slowly. A simpler explanation is that a greater diversity and complexity of evolving lineages survive mass extinctions than previously thought, and go on to rapidly seed the new course of evolution.

In high-resolution stratigraphic analyses (Kauffman, 1988a) of survival intervals for Devonian and Cretaceous mass extinctions (e.g. see Figs. 6-8), 17 successful biological strategies have been identified, to date, that have allowed lineages to survive mass extinctions (Fig. 10). Certainly more exist. Some lineages employ one strategy, others many. Collectively, these strategies insure that a genetically and ecologically diverse gene pool, mainly represented by small and isolated populations, will characterize the survival interval following mass extinction.

Major survival strategies identified in ancient mass extinction-recovery intervals by Harries and Kauffman (1990) and Harries (1993) (Fig. 10) include (1) *Ecological Generalists*: species with broad environmental tolerances and high stress resistance; (2) *Trophic Generalists*, with reliable food resources (e.g., organic debris); (3) *Ecological Opportunists*: broadly adapted species that produce high numbers of offspring to ensure the survival of a few, and which may rapidly occupy and proliferate in stressed habitats with low levels of biological competition; (4) *Disaster Species*: species that are specifically adapted to the stressed environmental conditions characterizing mass extinction intervals, but which otherwise exist in very small populations; (5) *Protected Habitat Dwellers*: species which normally live in habitats, such as the deep ocean, that are only slightly to moderately affected by the environmental stresses associated with mass extinction; (6) *Crisis Emigrants*: species which have the ability to migrate to secondary, more protected habitats (e.g., deep water, caves) during mass extinctions; (7) *Refugia Species*: species whose normal environmental range includes or is largely restricted to a refugium (e.g., caves, deep sea habitats) that is protected from the environmental stresses of a mass extinction interval; (8) *Cosmopolitan Species*: species having broad biogeographic dispersion, with subpopulations spread into, and even specifically adapted to, diverse, widespread environments that are little affected by the stresses causing mass extinction. (9) *Reproductive Survival Mechanisms*: Because the larval and juvenile stages of most species are the most environmentally sensitive to survival, certain reproductive strategies may give species higher survival potential: i.e. a large number of offspring; frequent reproductive episodes, very long intervals between reproduction; protective brooding of young; live birth of fully developed offspring; hermaphrodism, etc.; (10) *Ontogenetic Strategies*: e.g. developmental histories which include neoteny (limiting development to the most environmentally tolerant growth stage) or progenesis (speeding up development to a more environmentally tolerant adult stage), as a response to biological stress: (11) *Preadaptation*: species which have specific adaptations to environmental stress factors
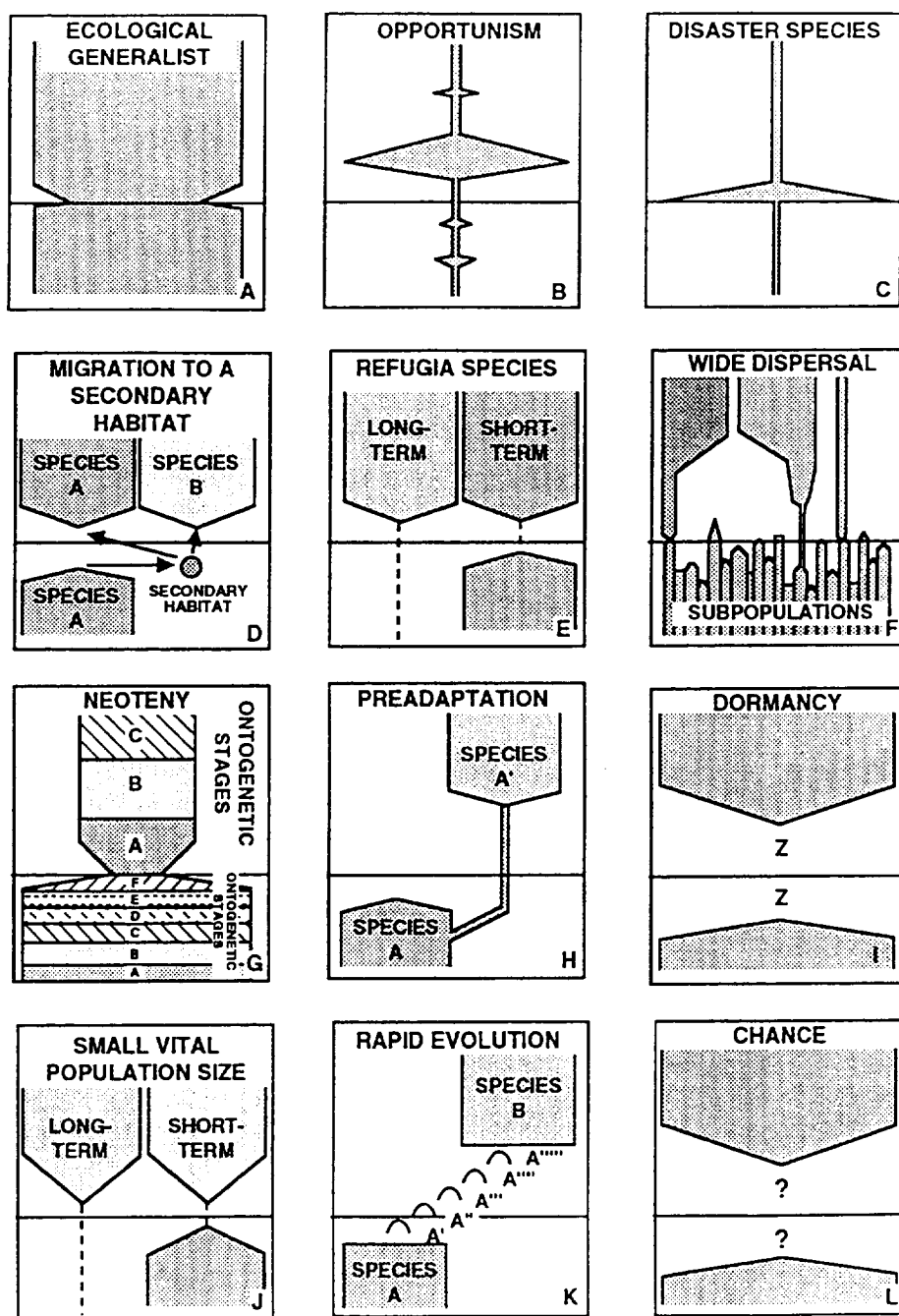
Figure 10 -- Models of common survival strategies for species, or larger taxonomic groups, that do not disappear during mass extinction intervals (modified after Harries and Kauffman, 1990; Harries, 1993). In each case the width of the patterned area represents the relative diversity and/or abundance of the group. Solid or dashed lines between patterned boxes represent the time when the species is very rare and surviving mainly in secretive habitats (refugia). Horizontal lines in all diagrams represent the major mass extinction horizon or interval. Different letters (A,B) indicate different species in the models, and A', A", A"', etc. indicate subspecies evolving within a lineage. See text for explanation of these strategies.

that characterize their normal habitats, and which may also characterize mass extinction intervals; (12) *Dormancy*: species with life histories which may include long resting or dormant stages (e.g. seeds, encystment, hibernation, etc.). (13) *Small, Viable Population Size*: Species which have a very small, critical population size for survival and reproduction, and for maintaining gene flow; (14) *Rapid Evolution*: Lineages of species which have the ability to undergo very rapid evolutionary change may be able to adapt to rapidly fluctuating environments that characterize many mass extinctions; (15) *Chemosymbiosis*: species which house chemoautotrophic bacteria in their tissues (bacteria capable of converting inorganic elements and compounds such as sulfur, sulfides, and methane to organic carbon and other useful materials) have a high survival potential, especially in times of low food resources and toxic chemistry. (16) *Inert Skeletal Composition*: species which utilize material other than calcium carbonate (e.g. silica, phosphate, protein) in building skeletons may have higher survival potential for mass extinctions which are characterized, in part, by rapid changes in the temperature and chemistry of the oceans, and/or by acid rain; and (17) *Chance*: "luck" may play an important role in survival, with vital individuals or populations of a species being in the right place at the right time to survive the principal environmental disturbances of a mass extinction.

Many of these strategies have been identified, or can be inferred, for the ancient survivors of mass extinction (Harries and Kauffman, 1990; Harries, 1993). These same strategies also provide living organisms with high survival potential. The diversity of life, and thus adaptive strategies employed in surviving the environmental stresses of a mass extinction, may directly relate to the overall diversity of life prior to the extinction event.

High-resolution stratigraphic, paleoenvironmental, and paleobiologic analyses of survival intervals following well-studied mass extinctions reveal three distinct survival stages: (1) a first stage coincides with the final, highly stressed phases of mass extinction and involves the early evolution of ancestral (progenitor) lineages that will survive and subsequently evolve to become important components of the post-extinction biotas; (2) the early part of the survival interval, immediately following the last main pulse of mass extinction, is characterized by population expansion (blooms) among surviving resident species, or "disaster species." (3) The final phase of survival within an area is characterized by population expansion and diversification among returning resident taxa and immigrant survivors from other regions or from refugia - so-called "Lazarus Species" (Fig. 11).

Within 250 Ky of most well-studied mass extinctions, evolutionary innovation begins, characterized by the rise of new species and lineages from surviving stocks. This initiates the RECOVERY INTERVAL (Fig. 11), characterized by rapid diversification of new biotas, macroevolutionary processes, and suites of new and innovative adaptive strategies. In fact, the greatest evolutionary innovations in the history of life may largely be the result of mass extinction, its effect on changing parameters of natural selecton, and the broad availability of empty ecospace to innovative evolutionary experiments during the ensuing survival and recovery intervals.
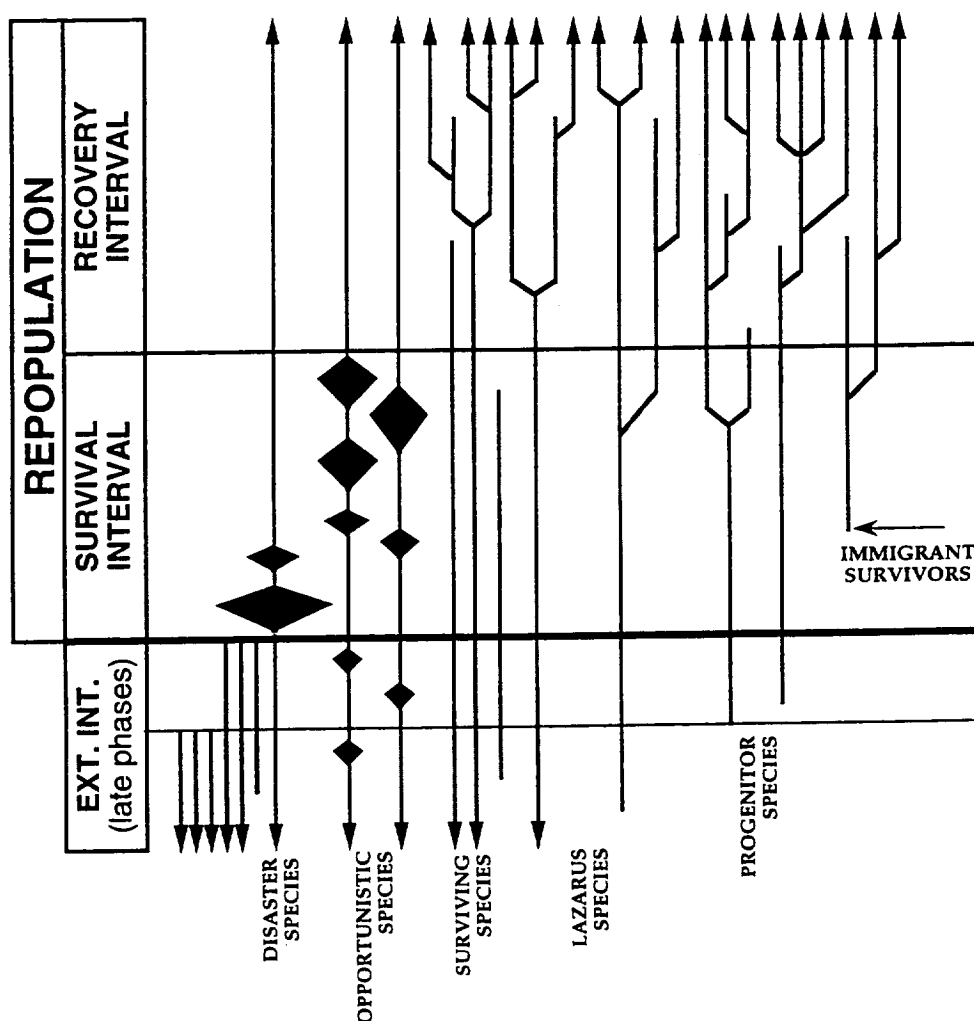
Figure 11 -- A model for the three phases of mass extinction events: *extinction, survival,* and *recovery* intervals (Harries and Kauffman, in manuscript). This diagram is based on a compilation of numerous paleontologic data bases from ancient mass extinctions. Each vertical black line represents a hypothetical species. Thin gray lines connecting black lines represent intervals where the species or lineage does not occur in the fossil record, although these species/lineages do survive (Lazarus effect). Branches in the black lines represent the evolution of new species. Swellings in the black lines represent short-term population "blooms" among species. Late phases of mass extinction are characterized by loss of species (lower left) as well as origins of *Progenitor Species* and temporary disappearance of *Lazarus Species* (discussed in text), both of which return during the survival interval. The *Survival Interval;* is characterized by population expansion among *Survivors,,Opportunists* and *Disaster Species,* which are specifically adapted to harsh conditions following mass extinction. Increased diversity, involving new species evolved from surviving and new lineages, characterize the recovery interval. These relationships suggest highly dynamic biological response to mass extinction events.

Initial observations from detailed stratigraphic and paleobiologic analyses of a limited number of mass extinctions, suggest that the recovery interval can be divided into two discrete phases: (1) an initial recovery interval, normally less than 500 Ky long, characterized by the evolution of new species from surviving lineages, and from the continued re-appearance of Lazarus species. This interval is marked by rapid evolutionary events which may be interrupted or even individually terminated by continued, smaller-scale, extinction events. Whereas origination of new species exceeds extinction during this interval, the continued role of extinction generally leads to a slow and irregular increase in biological diversity. (2) A final phase of the recovery interval, leading to the basic restructuring of major global ecosystems, is characterized by the evolution of new lineages and even major groups from surviving lineages - a time of maximum evolutionary innovation (radiation) - and by a more graded pattern of diversification during which extinction events play a relatively minor role (Fig. 11).

The survival and recovery intervals following well-studied mass extinction events reflect a time of low biodiversity during which life remains delicately perched on planet Earth. At the end of this 0.5-1 My interval, many basic ecosystems have been restructured in oceanic and terrestrial environments, but with the notable exception of the tropics, which takes 3-10 My for ecological recovery. Much of the remaining time between the end of the recovery interval, and the onset of the next mass extinction, some 25 or more million years later, seems to be characterized by the slow building of global biodiversity, and full recovery of diverse ecosystems, to equal or higher levels than those which existed before the previous mass extinction (e.g. Hansen, 1988).

LESSONS FOR THE FUTURE; THE MODERN BIODIVERSITY CRISIS AS VIEWED FROM THE PERSPECTIVE OF PALEONTOLOGIC MODELS

This leads us to the inevitable question: What will be the history of life on Earth, and of Man as a species, if we allow the current, exponentially increasing rate of human population expansion, global environmental decline, habitat destruction, and biodiversity loss to continue at present or accelerated rates? What will be the aftermath of the modern mass extinction?

Predictions from the geological record are frightening; for example, if the current rate of destruction of tropical rain forests and reef ecosystems continues, leading to their virtual extinction within one to a few centuries, the predictions of the geological record are that an average of 3-10 My will be needed before even basic tropical reef and rain forest communities will recover. Another 20 My will pass before these ecosystems will reach levels of diversity that preceded the impact of human beings beginning only 15 thousand years ago.

The detailed study of the fossil record during the phases of extinction, survival, and recovery associated with past global mass extinction intervals provides us with a powerful predictive tool for understanding, and reacting to, the modern environmental and

biodiversity crisis: it creates an awareness, and a perspective that we have never had. We must listen to the past.

What is the current situation on Earth (e.g. see Wilson, 1988)? Why do we, as paleontologists, believe that one of the greatest mass extinctions in the history of the Earth is now under way? Let us briefly examine some difficult issues and some hard facts.

1) Serious human influence on the modern extinction began between 9 and 15 thousand years ago on various continents with the advent of sophisticated hunting tools and the purposeful use of wild fire for herding and mass killing of larger animals. This, coupled with an abrupt climate change which may have weakened terrestrial ecosystems, led to a dramatic increase in extinction rates, and the first "step" in the modern extinction process.

2) The next phase of extinction and environmental decline initiated with the spread of the agrarian revolution during the last 2-3 thousand years, and especially during the last 500 years. This continues at an accelerated rate today to feed a dangerously expanding human population. The net effects of this historical phase have been the global destruction of vast areas of natural habitat for farming, increased erosion of exposed lands, increased turbidity and sedimentation rates in freshwater and marginal marine systems, the destruction of natural river courses and flow regimes, the lowering of groundwater tables, and dramatically reduced biodiversity due to "single crop" agriculture. Most recently, this phase has involved the poisoning of a huge diversity of species, including Man, through the use of insecticides, pesticides, fertilizers and growth hormones. This has been accompanied by the nutrification and ultimate "death" of lakes, rivers, and coastal waters and their biotas through the recycling of nitrate- and phosphate-rich agrarian fertilizers. This perturbation to the global ecosystem continues at an accelerated rate today.

3) A third phase of the modern mass extinction relates to the industrial revolution, >200 years old, and is characterized by further destruction of habitats in the quest for non-renewable natural resources. This phase also includes chemical pollution of air, water, and soils worldwide, increase in airborne particulate matter, the initiation of global warming, and the destruction of the ozone layer, with resultant climate change and increased radiation levels to Earth. This has accelerated today, forcing global environmental change, habitat loss, and lowering biodiversity by increasing extinction rates.

4) The historically youngest and most dangerous forcing mechanism for the modern mass extinction is overpopulation of the Earth by one aggressive species, Man. The global population is approximately 5.4 billion people today. This will more than double in the next century to over 12 billion humans at projected population growth rates, and this may be conservative. But the Earth is already beyond its carrying capacity for humans (2.4 billion) if we all had a standard of living that consisted of a small dwelling, with a single room, basic water and sanitation needs, and a diet consisting almost entirely of grains. If we acknowledge that a small proportion of the global population lives at a much higher standard, and most humans live at a much lower standard today, imagine what life on

Earth will be like in 100 years with over twice as many people. An overpopulated Earth means accelerated rates of natural habitat destruction, elimination of entire ecosystems (e.g., tropical rain forests), a dangerous lowering of biodiversity, and eventual depletion of non-renewable resources. If tropical rain forests alone are destroyed, we will lose over half of the diversity of life on Earth, and the modern mass extinction will be a statistical fact.

Already there are areas of the world where biodiversity loss during the last 15,000 years approaches or exceeds mass extinction levels. Most of the native larger mammals of Europe and North America are extinct or endangered; Africa is rapidly following. It is estimated that up to 60-70 percent of the native marsupial species of Australia are now extinct or endangered, as are over 50 percent of the primates of Madagascar, and up to 40 percent of the marine mammals. Global reef ecosystems are in shock and rapidly diminishing from coastal pollution, disease, overfishing, siltation, nutrification, and from excessive radiation levels related to the widening ozone holes.

But perhaps the most telling statistic is that projected for global rain forests, and especially those of the neotropics of South and Central America, and for Malaysia. Global biological diversity is variously estimated at 10 to 100 million species; many scientists suggest that 30 million species is a reasonable figure. Yet only about 1.4 million species have been described and studied; for the great majority, the benefits that these species might bring to humans (e.g., as sources for medicine) are completely unknown. Between 50 and 60 percent of these species are estimated to live in and marginal to tropical ecosystems, predominantly in rain forests. This represents half of the diversity of life on Earth. At present rates of habitat destruction, only 2-5 percent of the global tropical rain forests will be left by the year 2050, and less, if any, by the year 3000. The loss of this single ecosystem, among all of those on Earth, will result in biodiversity depletion on the scale of ancient mass extinctions, but at a rate that exceeds by magnitudes that of all past mass extinctions, including those related to the great meteorite impacts as at the end of the age of dinosaurs - the Cretaceous-Tertiary boundary.

Projected extinction rates on Earth today, and for the next 30 years, are 300 species lost per day, mostly microbes, but among them five plant species and one animal species. This is several magnitudes larger than that statistically projected for any ancient mass extinction.

CONCLUSION

The geological history of mass extinction, survival, and recovery during periodic biological crises on Earth can be studied at fine scales that approximate those used to monitor global change during the last 100 thousand years. These high-resolution studies initially demonstrate that mass extinctions and their aftermath, though multi-causal and complex, share significant characteristics. This allows us to develop a first set of predictive models concerning the rates, patterns, causes, and aftermath of mass extinction events, and to judge the role of biological diversity in assuring the continuance of life through

these global crises. These models, though preliminary and in need of extensive testing, forecast a dark future for our planet and its life should the overpopulation of *Homo sapiens*, the resultant global environmental crisis, and the spiraling rate of habitat destruction and biodiversity loss be allowed to broadly reach mass extinction levels. At current, exponentially increasing rates, this will take less than 100 years, within the lifetimes of our children and grandchildren. Without high levels of biodiversity, the global ecosystem will no longer be resilient to the environmental stresses associated with future mass extinction intervals, whether man-made, or naturally occurring some 12-14 million years in the future. The next mass extinction could be the most destructive of all.

The global community must realize that we are no longer looking into some futuristic crystal ball, or scanning the pages of science fiction in forecasting the demise of the global ecosystem, and the quality of life, as we now know it. We are looking into the eyes of our grandchildren and asking, "what will it be like for you in this dying world?" The decision is not theirs, it is ours, in this generation, at this moment. We cannot wait to gain the knowledge, and to make the bold personal, societal, and political moves necessary to reverse the spiraling rate of habitat destruction and biological extinction on planet Earth.

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The Search for an Extinction Event

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INTRODUCTION

Death of an organism is a very personal event. The extinction of a species is viewed as catastrophic, only if one is a member of that species. In fact, the extinction of a species simply represents the sum total of deaths of individuals within the species during a time interval in which the rate of death exceeds the rate of recruitment of new individuals. That is, the population size within the species declines to the point that the unit is no longer reproductively viable.

The classification of organisms is hierarchial. That is, each taxonomic level - species, for example - is nested along with other closely related forms within the next higher unit, here the genus. The cessation of any of the taxa above the species level marks the extinction of the last species within the taxon and, as such, may not be any more significant an event than the extinction of a species. Thus, when we state that the end of the Cretaceous is marked by the end of the dinosaurs, that is not to say that all dinosaurs became extinct at the end of the Cretaceous. Rather, it simply marks the point in time during which the last species of dinosaur ceased to be reproductively viable.

These events -- death of individuals, extinction of species, or termination of a higher taxonomic unit -- are all biologic events. They mark the truncation of a genetic lineage which has a profound and irreversible effect on the course of evolution.

The **pattern** of species extinction, however, may be viewed as a biological event on one hand and as an intellectual construct on the other. As described above, the extinction of all taxa has biological consequences. In all probability, most, if not all, extinctions could be assigned a cause. When one speaks of a pattern of species extinction, however, it is necessary to demonstrate that there is some temporal relation between the extinctions of various organisms and that these extinctions have a common cause.

We have known since the 19th Century that the rate of extinction has varied through geologic history and that certain periods of higher rates of extinction have coincided with time intervals in which major lineages disappeared. This is one of the primary bases for the development of the modern geologic time scale. It was not until the pioneering work of Raup and Sepkoski (1984; 1986) that there was an indication that this pattern, and perhaps the cause, of extinctions might be very different during "background intervals" and "extinction events." They determined that during several intervals of geologic time the rate of extinction of families and genera significantly exceeded the background level of extinction and that several of these extinction "events" coincided with the major breaks punctuating the geological time scale (Figure 1). The terminal Cretaceous event is one such extinction peak. As early as 1970, Digby McLaren suggested that one of these extinction peaks, that which occurred in the Late Devonian, might have been caused by impact of an extraterrestrial body. Yet it was not until the work of Raup and Sepkoski, in the 1980's, that this idea was given much serious consideration. They suggested that the major extinction events might be caused by extrinsic forces. Subsequently, Jablonski (1986) noted that if extinction events are catastrophic in nature, normal Darwinian selection processes may not function and that the susceptibility of species to extinction is related to its geographic range.

These are very exciting intellectual ideas that, fortunately, are quite testable. In order that these ideas be fully accepted, it is necessary to demonstrate that the evidence from the fossil record supports a different pattern, as well as rate, of extinction. Although the nature of this testing would seem to be obvious at the outset, it is complicated by the nature of the geological record and, as will be discussed below, some of the traditional methods of testing geological evidence for biological events may not be adequate.

Concomitant with the biological arguments that background intervals and extinction events might be different in origin, the first observations were also being published (Alvarez, et al., 1980) that an enriched iridium layer occurred at, or near, the Cretaceous/Tertiary boundary in a section exposed near Gubbio, in Italy. Because iridium tends to be depleted in the crust of the earth and because it occurs in higher proportions in extraterrestrial bodies, the presence of iridium in the rocks at Gubbio strongly suggested that the earth had been struck by an extraterrestrial body at that time. This quite reasonable conclusion was rapidly escalated into the "fact" that the earth had been struck by one or more bolides which caused
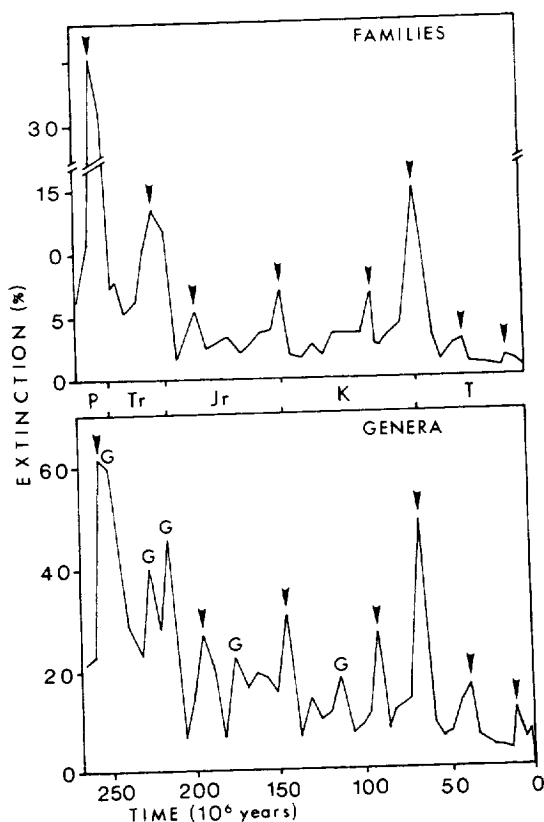
FIGURE 1--Plots depicting the rate of extinction of
families and genera from the end of the Paleozoic to
the Holocene. Arrows depict extinction events of a
magnitude significantly above the background level.
Peaks denoted by the letter "G" on the plot of generic
extinction represent periods of elevated rates of
extinction, measured at the generic level, that do not
coincide with those determined at the family level.
Patterns of extinction are extracted from Raup and
Sepkoski (1986).

the Cretaceous/Tertiary extinction. Thus, the extinction of
the organisms in this time interval was removed from the
biological realm to that of an astrophysical phenomenon. At
least in part because of the appeal of this idea, it was
very quickly endorsed by the popular press; this had the
effect of lending further strength and credence to the
theory. As a result, the burden of proof shifted from the
catastrophists to the gradualists, and the arguments and
tests for the extinction patterns, based purely upon
biological grounds, were either ignored or dismissed on the
grounds that the geologic record was an inadequate measure
of a geologically instantaneous event.

It is not appropriate to make the assumption that a bolide killed the dinosaurs and all other organisms that disappeared at the end of the Cretaceous, and **then** to seek proof for its documentation. Rather, it is critical that we examine the pattern of fossil remains in the geologic record and ask whether this pattern suggests an instantaneous, synchronous extinction of taxa or whether the extinction was a geologically short-term event with no particular, or necessary, cause of synchrony.

The test for an instantaneous extinction of organisms would seem obvious. Fossils are preserved throughout the stratigraphic record. If an extinction event occurred at the end of the Cretaceous, caused by a mechanism that resulted in instantaneous death of certain organisms, it would be predictable that the stratigraphic range of these organisms would abruptly end at that boundary. Unfortunately the fossil record is profoundly affected by events that occur subsequent to the death of organisms, collectively known as taphonomy. Many organisms are never buried, the remains are destroyed by processes of weathering and scavenging, and the organisms are not preserved in the fossil record. Others that are preserved may be subsequently destroyed by diagenetic processes such as solution and recrystallization, during or subsequent to the formation of sedimentary rocks. Still others may be destroyed as the enclosing rocks are weathered and exposed at the surface of the earth. Of course, not all fossils that are preserved will ever be found and examined. Thus, we do not have a complete picture of the geologic history of any previously living species. The record, instead, consists of isolated fossils so that the geological range of a particular species represents the span of time embraced by the sum of its occurrences (Figure 2). The degree of confidence that this range closely approximates the actual range is controlled by the number and spacing of stratigraphic occurrences.

When the geological range of organisms is expressed, it is done so in the terms of the geological time scale. For example, when an organism is said to have lived during the Maastrichtian, the last epoch of the Cretaceous, it is implied that the organism arose at the beginning of that epoch and became extinct at the end of it. There is no *a priori* reason to suggest that this is so. In fact, because of the problems of sampling the fossil record we can be almost certain that we will never find either the first representative or the last representative of any fossil species. The only basis we have for defining the range of fossil organisms is to record the precise positions of discovered fossils in the stratigraphic record. We certainly cannot conclude that, if an organism lived during
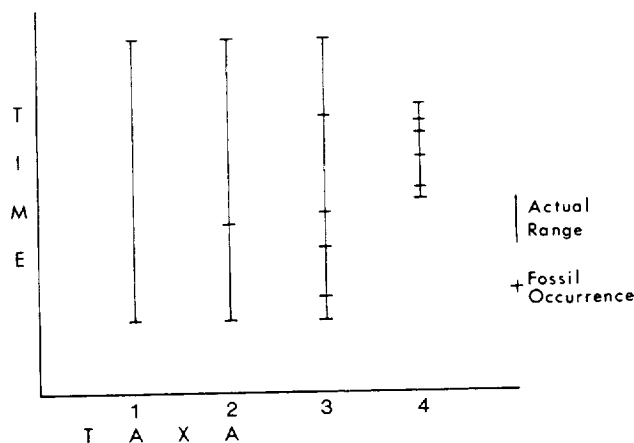
FIGURE 2--Stratigraphic ranges of four hypothetical taxa illustrating the manner in which ranges are determined. Note that, although the ranges of taxa 1-3 are the same, the range of taxon 3 is based upon several more occurrences than those of taxa 1 and 2. Thus, the confidence that the plotted range of taxon 3 approximated the actual range would be greater. The ranges of taxa 3 and 4 are based upon the same number of fossil occurrences but, because the range of 4 is substantially less than that of 3, the actual range would much more closely approximate the theoretical range in taxon 4. The same notations for actual range and fossil occurrence will be used in subsequent figures.

one moment of time within the Maastrichtian, it therefore lived throughout that epoch and became extinct at the close of the Maastrichtian.

Another interesting observation on the vagaries of the fossil record is the Signor-Lipps Effect. Signor and Lipps (1982) observed that because fossil are discontinuous in their distribution, sampling an extinction event that was truly catastrophic might, nevertheless, appear to be gradual (Figure 3). It would be highly unlikely that all of the organisms that became extinct would, in fact, be represented by one or more fossils right at the moment of extinction. Although the problems inherent in the Signor-Lipps effect can be mitigated by close-interval sampling, they can never be eliminated.
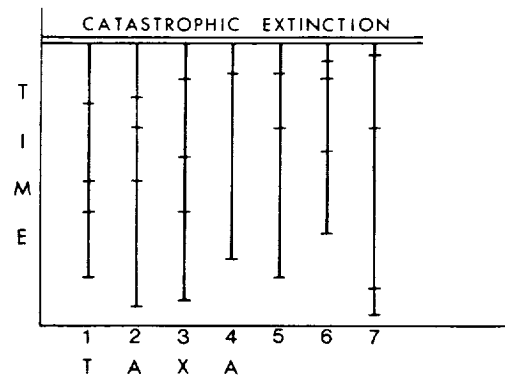
FIGURE 3--The Signor-Lipps Effect. Despite the defined condition that all seven taxa, in fact, became extinct at one instant in time, their fossil occurrences tend to indicate a gradual, or step-wise, extinction pattern.

Another set of problems that make it difficult to interpret an instantaneous geologic event is that of the incompleteness of the stratigraphic record. The accumulation of sedimentary rocks is not one of ceaseless, slow deposition of sedimentary grains within a depositional basin. Instead, virtually all sedimentary rocks are a result of accumulation of sediment at highly variable rates, ranging from long periods of non-deposition to relatively short intervals in which massive floods of sediment are deposited. Furthermore, once deposited, the sediments are not always preserved in their entirety. Processes of erosion can subsequently strip away previously deposited sediments, resulting in unconformities -- intervals of time not represented by a rock sequence. Periods of time during which sediments are not being deposited and periods of time during which unconformities are developing have the effect of artificially truncating the geologic range of organisms and, thus, giving the false impression of abrupt faunal changes (Figure 4). Unfortunately, many of the best known Cretaceous/Tertiary sections are characterized by slow rates of deposition of sediments and by unconformities (MacLeod and Keller, 1991a; b). These problems can be minimized by identifying geologic sections in which sediments accumulated rapidly, in an environment in which non-episodic, more or less continuous, sedimentation occurred, and with no evidence of erosional unconformities.

There are several other kinds of tests useful in distinguishing gradual from catastrophic extinction patterns which are not strongly affected by problems such as the Signor-Lipps effect. It is the purpose of this work to identify predicted biological patterns which should serve to define the tempo of the Cretaceous extinction event. In
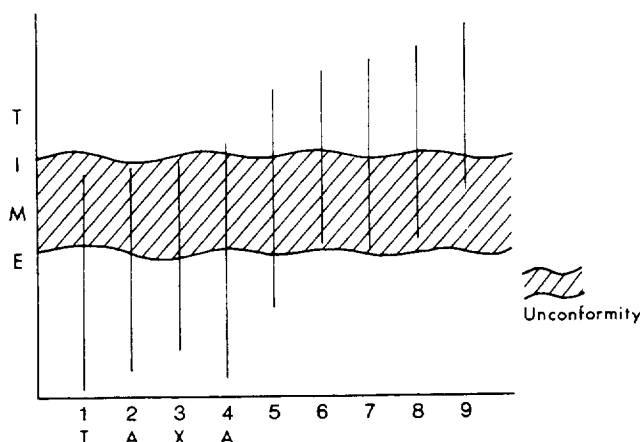
FIGURE 4--The effects of an unconformity produced by erosion of sedimentary rocks or non-deposition of sediments. Despite the fact that all taxa have overlapping ranges, the presence of the unconformity would lead to the conclusion that taxa 1-3 and 6-9 had non-overlapping ranges. Only taxa 4 and 5 would appear to overlap.

general, these tests will focus on inevitable results of a catastrophic extinction or will look for results which tend to negate a catastrophic extinction. To see how these patterns are expressed in the geological record, an exceptionally well-preserved and well-exposed section on Seymour Island, Antarctica, will be used as an example. I should emphasize that it is not the purpose of this work to evaluate the evidence for an extraterrestrial impact.

THE CRETACEOUS/TERTIARY BOUNDARY ON SEYMOUR ISLAND

Seymour Island lies on the eastern margin of the Antarctic Peninsula at latitude 64°15' S, and longitude 56°45' W (Figure 5). It lies within a cluster of islands, the largest of which is James Ross Island. Exposed sedimentary rocks range in age from Lower Cretaceous through the Eocene (Elliot, 1988). Seymour Island is the only one of these islands, and the only place in Antarctica, where the Cretaceous/Tertiary boundary is exposed. Despite its remote geographic position, Seymour Island is an outstanding site for the study of the Cretaceous/Tertiary boundary event. The general geological and paleontological framework of the island has recently been described (Feldmann and Woodburne, 1988) and the details of the Cretaceous/Tertiary
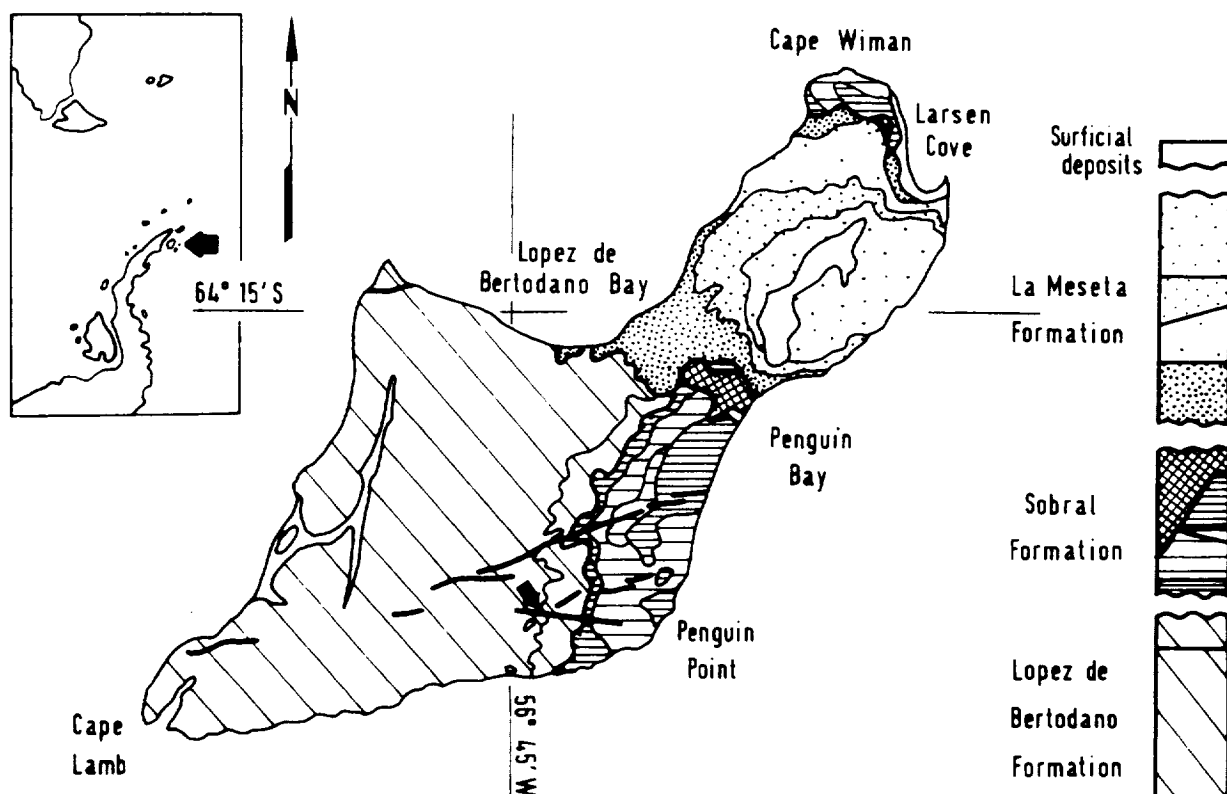
FIGURE 5--Geologic map and stratigraphic column of the
rocks on Seymour Island, Antarctica, showing the
position of the Cretaceous/Tertiary transition within
the López de Bertodano Formation. Map modified from
Sadler (1988).

transition interval have been documented (Zinsmeister et
al., 1989). The following descriptive material is taken
from these works.

The Cretaceous/Tertiary boundary lies within the López de
Bertodano Formation, a thick sequence of fine-grained
siliciclastic sediments which were deposited below wave base
in a continental shelf setting. Although it has not been
possible to make a precise determination of the rate of
accumulation of López de Bertodano sediments, the rate of
sedimentation appears to have been quite rapid. Based upon
Macellari's (1986) determination of ammonite zonation, the
sedimentation rate through the Maastrichtian is estimated to
be on the order of magnitude of 10 or more centimeters per
thousand years. If this is a reasonable estimate, the rate
of sediment accumulation may be as much as an order of
magnitude greater than the sedimentation rate across other

Cretaceous/Tertiary boundary sections that have been studied (MacLeod and Keller, 1991b). More important than the rate of sedimentation, the pattern of sedimentation appears to have been nearly continuous across the Cretaceous/Tertiary interval. No evidence of erosional events have been noted in the López de Bertodano sediments in the stratigraphic intervals spanning the boundary (Zinsmeister et al., 1989). Thus, from a sedimentary standpoint, the rocks represent an apparently complete sequence of relatively rapidly deposited sediments in a nearshore marine setting -- ideal for the study of the Cretaceous/Tertiary event.

The paleontological record is also extremely good. A rich and diverse assemblage of fossil plants and animals, both microfossils and macrofossils, has been collected from the rocks spanning the Cretaceous/Tertiary boundary. The macrofossils, while dominated by molluscs including ammonite cephalopods, include representatives of nearly all phyla commonly preserved in the fossil record. The fossils are abundant and extraordinarily well-preserved. Furthermore, there is no evidence that the fossils have been transported any substantial distance prior to burial. Surfaces of the specimens show little, if any, abrasion and bivalved molluscs are often found with the valves conjoined.

Decapod crustaceans are often preserved in concretions which are found in specific stratigraphic horizons. The concretions have not been transported from these stratigraphic horizons and, if the concretions have been opened by weathering processes upon exposure at the surface, the two halves of the concretions tend to be found lying beside one another. Thus, little or no transportation of fossil material has occurred subsequent to exposure.

Microfossils are similarly well preserved. A rich assemblage of dinoflagellate cysts (Askin, 1988), diatoms (Harwood, 1988), and foraminiferans (Huber, 1988) have been described. Therefore, the fossil record across the Cretaceous/Tertiary boundary on Seymour Island is as rich and diverse as any other section known to span this time interval. The details of the fossil distribution are discussed below.

BIOLOGICAL PATTERNS DURING EXTINCTION EVENTS

Faunal Diversity

The pattern of extinctions should be markedly different in catastrophic as opposed to gradualistic extinction events. If, for example, one were to describe a catastrophic extinction as one in which the effects were

expressed over 10s or even 100s of years, it would be predicted that the extinction of organisms should be confined largely to this time interval (Figure 6). Some extinctions, however, might occur subsequent to the catastrophic event as the effects of the earlier extinctions and the catastrophe ripple through the ecosystem. It would not be predicted that any of the organisms becoming extinct as a result of the catastrophe would have done so prior to the moment of extinction. Furthermore, that moment of extinction, particularly with reference to the "index" taxa defining our geologic time scale, would have to be demonstrated to be synchronous world-wide and across terrestrial and marine habitats. The Cretaceous/Tertiary boundary has been variously defined, historically, on the basis of the extinction of dinosaurs, terrestrial plants, ammonites, rudistid bivalves, foraminiferans, and
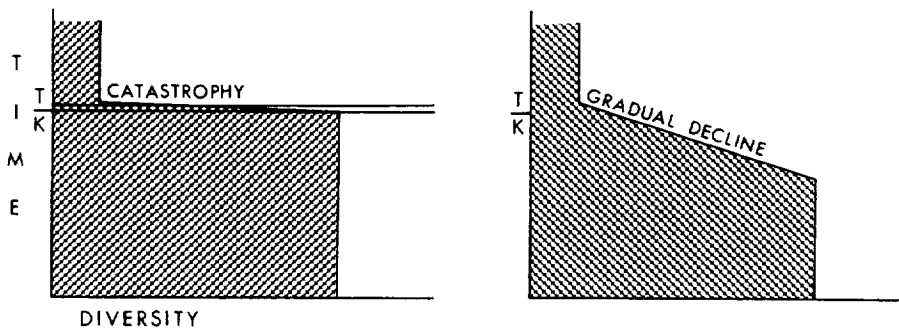
FIGURE 6--Plots of theoretical patterns of decline in numbers of taxa resulting from catastrophic (left) and gradual (right) extinction events.

dinoflagellates, among others. These organisms inhabit a broad spectrum of ecological niches, and all would have to be affected synchronously. On the other hand, if the extinction of these organisms was triggered by non-catastrophic forcing mechanisms which might span thousands or hundreds of thousands of years, or more, then simultaneous extinction of these taxa would not necessarily be predicted (Figure 6). What one would predict would be a geologically rapid decline in total diversity of organisms resulting from the sum of extinctions of individual groups, each perhaps responding to different forcing mechanisms.

Examination of the last occurrence of fossils in the stratigraphic record is the most typical and traditional of the methods used for determining extinction patterns and, of course, is the one that is used primarily in defining the geological time scale. The method is fraught with the problems inherent in interpreting the sedimentary and

paleontologic record, including those of the Signor-Lipps effect, unconformities, and the vagaries of preservation of fossils. Nonetheless, the method will, and must, continue to be used to examine the fossil record unless we conclude that the paleontological record is simply not adequate to assess biological history. That is, of course, nonsense.

There are several conditions that, if satisfied, can minimize the problems of preservational history of fossils. Continuous rapid deposition of sediments would have the effect of making it possible to develop a more precise interpretation of a stratigraphic range of fossils. Close-interval sampling of fossils would, in turn, serve to refine the stratigraphic ranges and, therefore, reduce the Signor-Lipps effect.

The Cretaceous/Tertiary boundary sequence of megainvertebrates on Seymour Island (Figure 7), plotted according to their last occurrence in the section, illustrates a pattern that can only be interpreted as a gradual, long-term pattern of disappearance of taxa from this section. The shaded area, defined by the interval of time during which the greatest decline in taxa occurs and including the disappearance of foraminiferans, dinoflagellate cysts, and ammonites, spans almost 30 meters of the stratigraphic interval. Within that same section, an iridium enrichment horizon has been identified, based upon exploratory sampling. Several observations can be made from these data. If one estimates the sedimentation rate to be on the order of 10's of centimeters per thousand years, the time span of the transition interval from Cretaceous to Tertiary faunas would be hundreds of thousands of years. The index taxa used to identify the Cretaceous/Tertiary boundary worldwide span this 30 meter interval of section. It is also clear that many taxa not considered to be index taxa disappear well before that transition interval and others disappear upward in the section subsequent to the transition interval. The precise stratigraphic position of each of the fossils referred to the taxa is plotted on the stratigraphic distribution of those taxa. It suggests that the plotted stratigraphic ranges are reasonably well defined. A similar pattern of distribution has been demonstrated in other groups including diatoms (Harwood, 1988), and dinoflagellate cysts (Askin, 1988). Thus, it is clear that the disappearance of taxa from this section is gradual and that the greatest rate of disappearance of taxa, encompassing the entire interval during which index taxa became extinct, spans 30 meters of section. Certainly, there is no evidence to suggest that a catastrophic extinction event occurred, based upon these data.
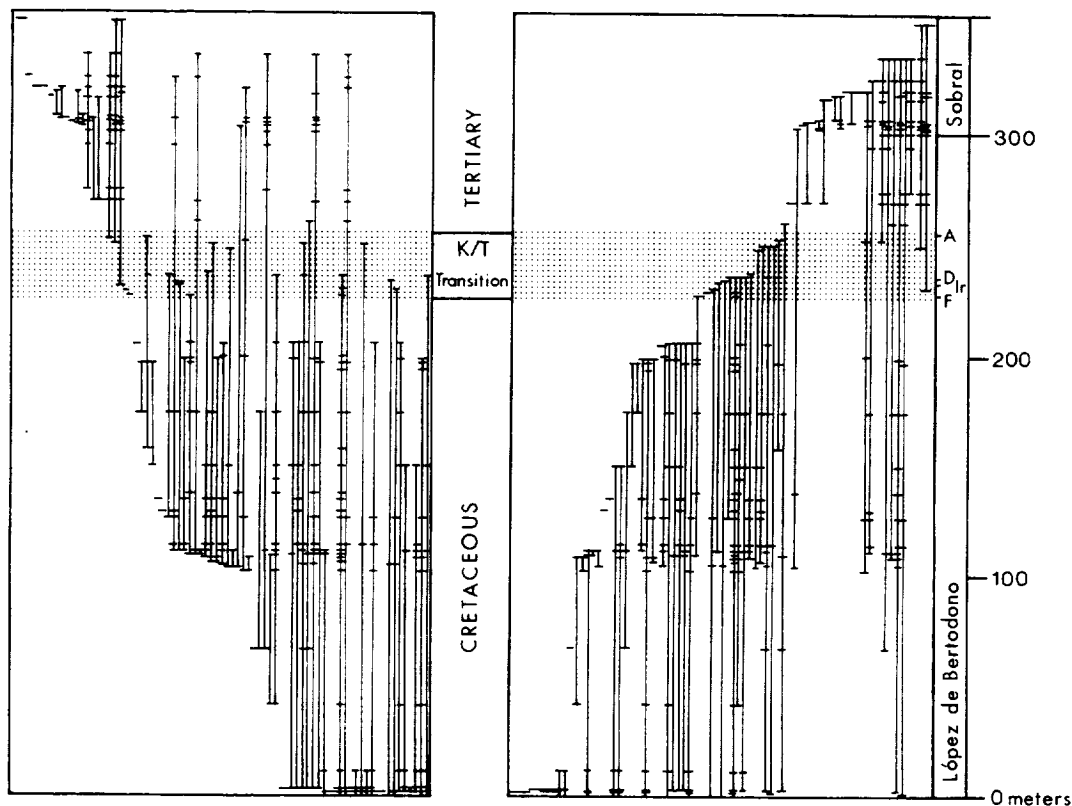
FIGURE 7--Actual ranges of 77 megafossil species
collected along section C (Macellari, 1984a) arranged
according to first occurrence (left) and last
occurrence (right) in the section. The position of the
last ammonite (A), the Cretaceous/Tertiary boundary
based upon dinoflagellates (D), the last Cretaceous
foraminiferans (F), and the iridium anomaly (Ir) are
indicated within the transition zone. Plots simplified
from Zinsmeister et al. (1989).

Numerical Abundance of Fossils

The numerical abundance of fossils in any stratigraphic
section is based upon several factors, including the living
population size, the rate of death of organisms within that
population, and a variety of taphonomic and diagenetic
factors. In order to analyze the tempo of extinction of
organisms it is possible to define three generalized
patterns of numerical abundance of fossils, assuming no
substantial change in taphonomic or diagenetic history.

If a living population is characterized by a constant

number of individuals over a certain interval of time, one
would conclude that the number of deaths of individuals is
equalled by the number of recruits into that population.
That is, the standing population would remain constant. The
number of fossils that would potentially be preserved from
this population would be a very small percentage of the
number of individuals dying (Figure 8 left) and, in fact,
might have nothing to do with the standing population. For
example, if the death rate of a standing population was very
high and the recruitment rate was very high offsetting the
death rate, the number of organisms entering the fossil
record might be very high; conversely, if the death rate and
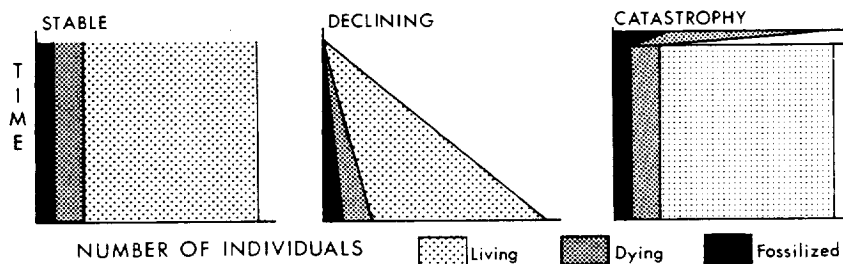
FIGURE 8--Plots depicting the theoretical pattern of
    numbers of individuals living, dying, and fossilized
    within populations characterized by stable numbers of
    individuals, declining numbers of individuals, and a
    stable population suffering a catastrophic extinction.

corresponding recruitment rate was very low, fewer
individuals would contribute to the fossil record. In
either case the number of fossils potentially preserved
would remain constant through the time interval.

On the other hand, if the population was in decline over
the same interval of time, one would conclude that the rate
of death exceeded the rate of recruitment. The standing
population would be in decline and, following the same
reasoning, the number of individuals entering the fossil
record would decrease up-section (Figure 8 center).

The pattern would be quite different, however, in the
case of catastrophic extinction. Once again the number of
fossils that one would expect to be preserved would be some
function of the number of individuals dying, rather than the
number of individuals living within the standing population.

At the moment of a catastrophic extinction, 100% of the
standing population would become extinct and the record of
that extinction should be reflected as a marked increase in
the number of fossils preserved (Figure 8 right). This
spike in numerical abundance should be one of the most
obvious, and most widespread, signals of a catastrophic
extinction. In marine habitats, vast shell accumulations
often have been attributed to mass mortalities; and, it
would be unthinkable to postulate a mass mortality event in
the absence of an unexpectedly great accumulation of
fossils.

Examination of the Cretaceous/Tertiary transition
interval on Seymour Island documents no such layer
indicating a mass mortality. In fact, the entire
stratigraphic section is richly fossiliferous; inspection of
the section gives no indication of a massive change in
numerical abundance of fossils that could be attributed to
any sort of catastrophic event. Although this has not been
tested rigorously, the Cretaceous/Tertiary boundary can be
traced over several kilometers on Seymour Island and at no
place has the fossil record captured such an event. Thus,
an examination of the numerical abundance of fossils
preserved in the Seymour Island section gives no evidence of
catastrophic extinction of any of the taxa that disappear
throughout that stratigraphic interval.

Pattern of Recruitment of Replacement Taxa

If a catastrophic extinction event were to have occurred,
one would anticipate that recruitment of taxa, replacing
those lost during the extinction event, could not begin
during the time interval preceding the extinction event.
That is, niches made available by taxa becoming extinct
would not be available until after the extinction had
occurred and, therefore, the individuals occupying those
niches should not appear in the stratigraphic record prior
to the extinction (Figure 9). If the recruitment occurred
throughout pre- and post-extinction time, it would suggest
that the extinction event would better be described as a
turnover rather than as a catastrophic change.

This latter pattern of turnover is observable within the
Seymour Island section. The stratigraphic distribution of
megainvertebrates (Figure 7), dinocysts (Askin, 1988), and
diatoms (Harwood, 1988) plotted according to appearance in
the stratigraphic interval, rather than disappearance,
clearly demonstrates that recruitment of the taxa which
dominate the Tertiary portion of the López de Bertodano
Formation occurred throughout the stratigraphic section. In
fact, the observed decline in taxa across the
Cretaceous/Tertiary boundary represents the sum of the

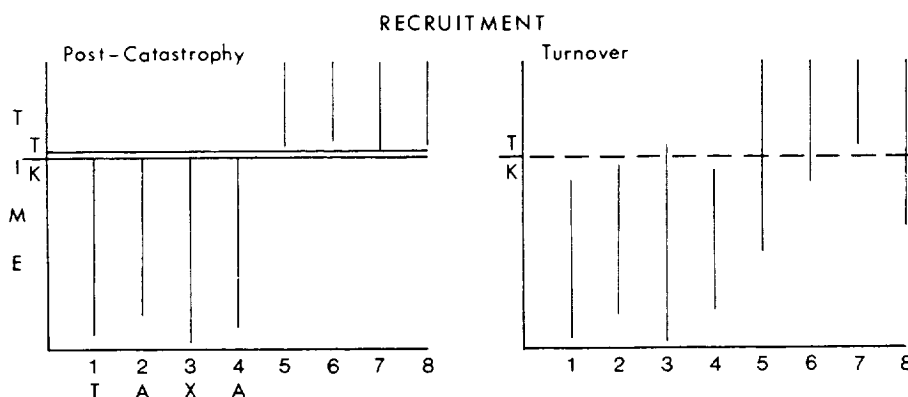extinctions of organisms and the recruitment to the fauna (Figure 10).

FIGURE *9*--Predicted patterns of addition of new species replacing species in older populations following a catastrophic extinction event and during a gradual turnover in taxa.

Note that, where the number of organisms becoming extinct tends to increase across the transition interval, the number of new recruits remains essentially constant. There is no evidence of an abrupt increase in the number of recruit taxa following the extinction event. One is left with the conclusion that there is no evidence for a catastrophic event in these data.

Selectivity of Extinctions

If the impact of one or more extraterrestrial bodies be considered a viable cause of the Cretaceous/Tertiary extinction, it would demand that there be an effect strong enough to result in the extinction of ammonites, micro-organisms, and dinosaurs, among others, on a global scale. These organisms were distributed over nearly the entire planet at the end of the Cretaceous. Numerous scenarios have been considered, including a "nuclear winter" and complete collapse of the food web. In fact, just such a devastating event would probably be necessary if all these various organisms were to be extinguished simultaneously. However, many groups of organisms, living in intimate association with those that became extinct, did not suffer extinction. The pattern of extinction was quite selective.

A broad range of possible biotic responses to a catastrophic event have been presented. Rhodes and Thayer (1991) suggested that, presuming the extinction resulted
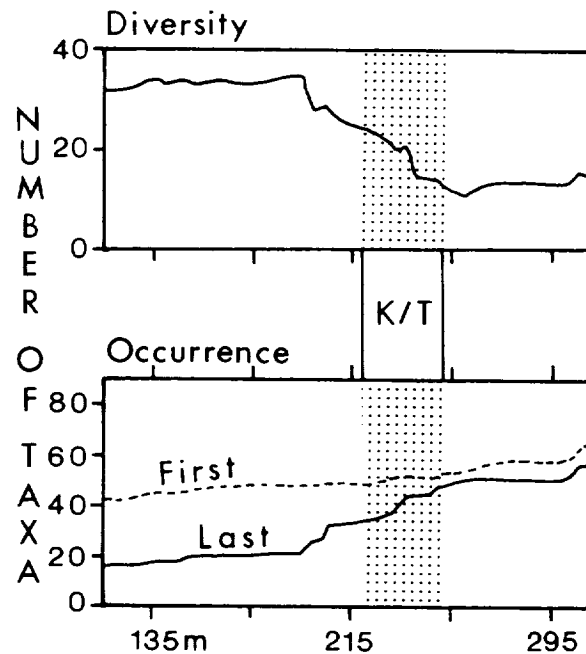
FIGURE 10--Changes in number of species of megafossils identified along a transect of Macellari's section C (1984) depicting a gradual decline in diversity preceding and through the transition zone (upper) and the pattern of numbers of first occurrences and last occurrences along the same transect (lower). Note that, whereas the pattern of last occurrences nearly mirrors the pattern of total diversity, the plot of first occurrences remains largely unchanged. Modified from Zinsmeister et al. (1989).

from a collapse of the food web, those organisms that were highly susceptible to changes in food availability would be most severely affected. Landman (1984) evaluated the reproductive strategy of nautiloid and ammonoid cephalopods and concluded that the ammonoids were more vulnerable than were the nautiloids in this regard. These approaches are all based upon the assumption that the extinction was a response to the processes of natural selection. That is, the catastrophe resulted in such a severe environmental perturbation that many organisms were neither able to tolerate and survive the change nor to adapt.

A totally different approach was suggested by Jablonski (1986). He postulated that during periods of sudden, enormous environmental stress normal processes of natural

selection would be overridden. Under these circumstances, those organisms that would tend to be survivors would be those with the broadest geographic range. It would not matter whether the organisms were ecological generalists or specialists. Processes interpreted within the context of natural selection would be operative during periods of background extinction but not during the period of catastrophic stress.

Thus, it is clear that there is no simple scenario for the role played by ecological flexibility and survivability. It is highly likely that both ability to tolerate ecological stress and geographic distribution would be important in any time of severe ecological change. However, strict resolution of the question is necessary only if the burden of proof is strictly on the gradualists. Examination of the fossil record provides no tangible evidence either of collapse of the food web or of total, worldwide destruction.

Examination of the fossil record on Seymour Island shows that nearly all groups of organisms suffered extinction to some extent but that, with the exception of the ammonites and marine reptiles, all the groups experienced turnover of taxa and no particular trophic group, within phyla or classes, was particularly hard hit (Feldmann and Woodburne, 1988).

SUMMARY

It is possible to distinguish between catastrophic and more gradual extinction patterns in the geological record, despite the incompleteness of the record and the problems inherent in it due to discontinuous sedimentation, erosion, and the Signor-Lipps effect. Four patterns of distribution can be analyzed: the pattern of extinction of taxa, the numerical abundance of taxa in the stratigraphic record, the pattern of recruitment of new taxa, and the selectivity of the extinction. Examination of the fossil record on Seymour Island, Antarctica, provides evidence that extinction and recruitment patterns occurred throughout the stratigraphic section from well below to well above the Cretaceous/Tertiary boundary, and that the turnover of taxa from typical Cretaceous forms to typical Tertiary forms was gradual and transitional. The numerical abundance of fossils throughout the section did not noticeably increase through the transition interval and, certainly, no mass mortality event is recorded. Individual taxa viewed as indices to the end of the Cretaceous, including foraminiferans, dinoflagellate cysts, and ammonites, are well preserved in the sequence and disappear from the record at very different places throughout the 30 meters of

stratigraphic section characterizing the transition. There is absolutely no evidence for a catastrophic extinction of organisms in this section. Finally, these observations are not unique to the Seymour Island region. Cursory analysis of the data describing fossil distributions in other Cretaceous/Tertiary sections around the world (Keller, 1989; Ward, Wiedmann, and Mount, 1986; Ward et al., 1991) similarly suggest decline of Cretaceous taxa over long spans of time and provide no clear evidence of a catastrophic event. Thus, the fossil record seems to provide no evidence of a cause and effect relationship between the possible impact of the earth by an extraterrestrial body or other catastrophic event and the Cretaceous/Tertiary extinction.

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What Can the Fossil Record Tell Us About the Terminal Cretaceous Extinction Event and the Disappearance of the Dinosaurs?

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INTRODUCTION

During the past decade, the scientific community, media and general public have witnessed one of most fascinating scientific debates of the century concerning the extinction at the end of the Cretaceous that resulted in the demise of the dinosaurs. It is doubtful that, if dinosaurs had not been among the principal characters, the Terminal Cretaceous Extinction Event (TCEE) would have received such close attention. The fact that so much attention has been given to dinosaur extinction when in fact, they played only a minor role in the TCEE, has shifted the focus away from more fundamental unresolved questions concerning this profound biotic event 65 mya (million years ago).

Dodson and Tatarinov (1990) proposed four questions in their discussion of the extinction of the dinosaurs; these questions are equally applicable to the entire question of the TCEE:

1. Can dinosaur extinction be considered by itself, or must it be considered in the context of extinctions of all contemporaneous plants and animals both in the sea and on land?
2. Was extinction of the dinosaurs sudden and catastrophic (measured in hours, days, weeks, or months), or was it slow and gradual (100,000 years, a quarter of a million years, or even a million years or longer), culminating a long period of decline in diversity and biomass?
3. Can the Terminal Cretaceous Event be considered by itself, or must it be considered in context with other periods of mass extinctions in the Earth's history?
4. Are terrestrial agents sufficient to account for extinctions, or should astronomical causes be sought?

The first question is the most important, and in itself provides the reason why early hypotheses concerning dinosaur extinctions or other extinction events have never gained widespread support. Although dinosaurs are the best known animals to have become extinct at or towards the end of the Cretaceous, they actually comprised only a small percentage of the total number of life forms that died at this time. If we are to understand the TCEE, it is necessary to find a mechanism that explains not only the extinction of the dinosaurs, but also other extinctions in both the terrestrial and marine realms.

Although hypotheses concerning the TCEE have been proposed for more than 100 years, no theory ever has acquired widespread support in the scientific community. Early hypotheses fell into one of two broad categories: specific agents to explain the extinction of individual groups, such as the dinosaurs, or broad generalizations based upon terrestrial or cosmic global environmental perturbations. Each of these early hypotheses have failed because they either focused on a specific agent that may have affected single groups of organisms rather than the entire extinction event; or, in the case of global environmental perturbations, were based on faulty premises, unique untestable events, or the absence of supportive data.

Renewed interest in the TCEE was initiated by the 1980 publication of the Asteroid Hypothesis by Luis Alvarez and his colleagues. The seductive aspect of the impact hypothesis is that it provides a single mechanism for extinction in both the terrestrial and marine realms. Although impact hypotheses have been suggested in the past, there was little supportive data. In contrast to earlier impact hypotheses, Alvarez's hypothesis was supported by, what appeared to be, a compelling new set of physical data - the occurrence at a number of Cretaceous/Tertiary (K/T) sections of an enrichment horizon of the rare earth element, iridium, at the boundary between the latest Cretaceous and the Tertiary.

The catastrophic nature of the Alvarez impact hypothesis generated enormous media attention and swift reaction within the scientific community. One faction consisting of quantitative physical scientists accepted the hypothesis as gospel, and believed further that it might be the ultimate driving force of organic evolution. However, most of the paleontological community believed that the data simply did not support the hypothesis as presented, and subconsciously felt that the idea violated the basic foundations of geological and biological sciences - Actualism and Natural Selection.

Both factions immediately began to muster data to support their respective positions. As a consequence, the geosciences have undergone a revolution, not only in the way the TCEE was viewed but, more importantly, in the quest for new types of data and evaluation of how these data were collected. Within a brief period the debate became polarized, with the media playing a greater and greater role, not only promoting one particular view, but also as a means of attacking any opposing points of view or opponents. This polarization and rancor that has been introduced into the debate has been unfortunate and counterproductive in our quest to really understand this major biologic event in the history of life.

An ultimate understanding of the massive extinction event at the end of the Cretaceous does not, nor will, rest solely upon physical lines of evidence supporting either the impact or volcanistic hypotheses but rather, will ultimately come from an understanding of biotic events as recorded in the fossil record. This paper will focus on how biotic

patterns observed in the fossil record can be used to decide which, if either, of the current hypotheses is correct.

REVIEW OF IMPACT AND VOLCANIC HYPOTHESES

The Asteroid Hypothesis as proposed by Alvarez et al. (1980) is based on the impact of an asteroid approximately ten kilometers in diameter. The resulting cataclysmic explosion produced a dust cloud that was quickly carried by atmospheric winds around the Earth blocking out sunlight, leading to what could be termed the "**Lights Out Effect**." The blocking out of sunlight resulted in the wholesale destruction of the photosynthesizing producers at the base of the food chain, both on land and in the sea. The destruction of the primary producers set into motion a chain-reaction of death by starvation that cascaded through the higher levels of the food chain. This scenario appeared to provide a viable mechanism to explain widespread extinction in both the marine and terrestrial realms at the end of the Cretaceous.

Almost immediately after publication of the Alvarez hypothesis, a number of papers, many of which were based on little or no data, were published describing possible after-effects of such an impact. These models, if correct, would seem to provide compelling evidence for the catastrophic nature of the impact event and the extinction at the end of the Cretaceous. The following summarizes the most popular of the after-effect hypotheses:

1. Global Conflagration - The presence of soot-like carbon particles at the K/T boundary has been cited as compelling evidence of global wildfires that may have been started as a consequence of the heat generated by the impact (Wolbach et al., 1985). These fires are believed to have swept across the face of the Earth consuming everything in their paths, including the last fleeing herds of screaming dinosaurs. It is surprising that such a widespread conflagration produced no geomorphic signature, such as a record of increased erosion of the denuded world or corresponding deposition in the marine record.

2. Broiler Effect - A variation of the global forest fire scenario has been presented by Melosh et al. (1990). In this model, enormous quantities of ejecta were hurled above the atmosphere at suborbital velocities, causing a meteor shower of epic proportions, as debris rained back down through the atmosphere. The heat generated by this post-impact meteor shower is believed to have elevated atmospheric temperatures to a level well in excess of 550 degrees C for an extended, but unspecified period of time. In addition, the intense heat generated by the meteor shower would also have aided in the ignition of the global forest fires.

3. Wicked Witch of the East Effect - Lewis et al. (1982) and Prinn (1985) suggested that the elevation of atmospheric temperatures by the impact, meteor shower, and global forest fires resulted in combining of atmospheric nitrogen with water vapor to form nitric acid, leading to an acid rain of truly epic proportions. The recent

suggestion that the impact may have been in an evaporite-rich sequence in Central America have led some investigators to propose that, in addition to nitric acid, substantial amounts of sulfuric acid may also have been formed immediately after the impact event. The resultant acidification of the seas is envisioned as having had a devastating effect on all calcareous shelled organisms, metaphorically similar to the dissolving of the Wicked Witch of the East in the Wizard of Oz.

4. Stangelovian Oceans - The apparent absence of a crater led Hsu (1980) and Hsu et al. (1982) to propose a marine cometary impact that resulted in the formation of a Stangelovian Ocean. Hsu suggested that after-effects of such an impact event would have been a poisoning of life in the seas with CN, CO+, CH, NH, and OH. In addition, vast quantities of extraterrestrial CO^2 were released into the atmosphere by disintegration of the comet. The virtual elimination of photosynthesizing plankton would have also increased the amount of CO^2 entering the atmosphere, leading to a greenhouse warming of as much as 4°C (Hsu et al., 1989). This post-impact greenhouse effect is believed to have lasted as long as 50,000 years, severely stressing the terrestrial biosphere and leading to extinction of the dinosaurs and other groups of terrestrial organisms. If this scenario is correct, mass extinction in the sea would have preceded the terrestrial mass extinction.

5. Veil of Death Effect - As the global wildfires burned themselves out, vast quantities of smoke and ash, together with dust and debris from the impact, would have effectively blocked out all sunlight and plunged the Earth into a veil of frozen darkness for a period lasting months or years. Any survivors of the holocaust immediately following the impact would have slowly died either by starvation or of emphysema during this **"Night of the Living Dead."**

If this apocalyptic scenario is correct, it is no wonder that there was a catastrophic extinction of the dinosaurs, ammonites, marine phytoplankton and marine reptiles at the end of the Cretaceous. However, one also naturally might ask, how could any living thing have survived such an cataclysmic event as proposed by proponents of the impact hypothesis?

VOLCANIC HYPOTHESIS

The most plausible alternative theory yet to emerge is based upon the effects of massive volcanism that occurred at the close of the Cretaceous, and continued into Tertiary time in India. For a period of several million years during the latest Cretaceous, a truly massive episode of volcanic activity occurred to form the Deccan Traps. During this eruptive episode, vast quantities of volcanic gases (principally carbon dioxide) were released into the atmosphere (Courtillot et al., 1988). As a consequence, the composition of the atmosphere was altered, which eventually led to a corresponding rise in atmospheric temperature, change in the chemistry of rainfall, and eventually in sea water chemistry. Although most Deccan volcanism occurred as quiet outpourings of flood basalts, there were periods of violent eruption, supposedly accounting for as much as 10

to 15 percent of the total volume of the trap rocks. Injection of vast amounts of dust into the atmosphere, as a consequence of these violent volcanic episodes, would block out or greatly reduce incoming sunlight. This disruption of photosynthesis would result in a collapse of the food chain, in what could be termed the "Curse of Pele."

Although I shall not dwell on detailed pros and cons of the differing hypotheses, either would have had a catastrophic effect on the atmosphere and water chemistry of the sea, leading to a profound disruption of the biosphere. The major difference between the two hypotheses would be in the rate of environmental disruption. Effects of an impact event would have been virtually instantaneous (days, months, or a few years), whereas a volcanic generated catastrophe would have an extended or relatively long, but geologically-short period of time (10's, 100's or several million years), with effects varying as a consequence of waxing and waning volcanic activity. For either hypothesis to be accepted as the correct mechanism for mass extinction at the end of the Cretaceous, the following conditions must be met: First, there must be direct physical evidence for either event at the end of the Cretaceous, and more importantly, the event must be shown as being the direct cause of the TCEE.

PHENOMENON OF EXTINCTION

With any discussion of the role of the catastrophic extinctions on the history of life, it first is necessary to examine the requisite phenomena of extinction: types, underlying causes, and rates of extinctions. Simpson (1983) pointed out that extinction of organisms is not as simple and straight- forward as commonly believed. Species, like individuals, are born, rise to a peak of abundance and distribution, decline, and eventually die. Each species has its own unique evolutionary cycle and pattern. A salient feature of evolution is the trend towards specific specialization. An evolutionary premium is placed on specialization or adaptation to a particular set of environmental conditions: the greater the adaptation, the greater the survival potential of a species. This trend toward greater specialization also results in an evolutionary paradox: high specialization invariably leads eventually to extinction. The critical factor in this evolutionary paradox is environmental stability. In a stable environment, survival is enhanced by increased specialization. In a changing environment, an evolutionary premium is placed on less specialized organisms that have a high degree of adaptability. Thus unspecialized organisms inherently have a greater potential to adapt to changing environments. Simpson (1944) referred to this phenomenon as the "survival of the relatively unspecialized."

TYPES OF EXTINCTION

Simpson (1949) recognized two types of extinction: **pseudoextinction** and **terminal extinction** (Figure 1). Pseudoextinction is the consequence of evolutionary change in which morphologic changes are so great that the descendent no longer resembles the ancestral form. The ancestral species has become extinct, but the evolutionary lineage

continues. Terminal extinction occurs when highest specialized forms cannot adapt to new conditions, and thus become extinct terminating the evolutionary lineage. Unfortunately, few authors distinguish between the two types of extinction when presenting their data.
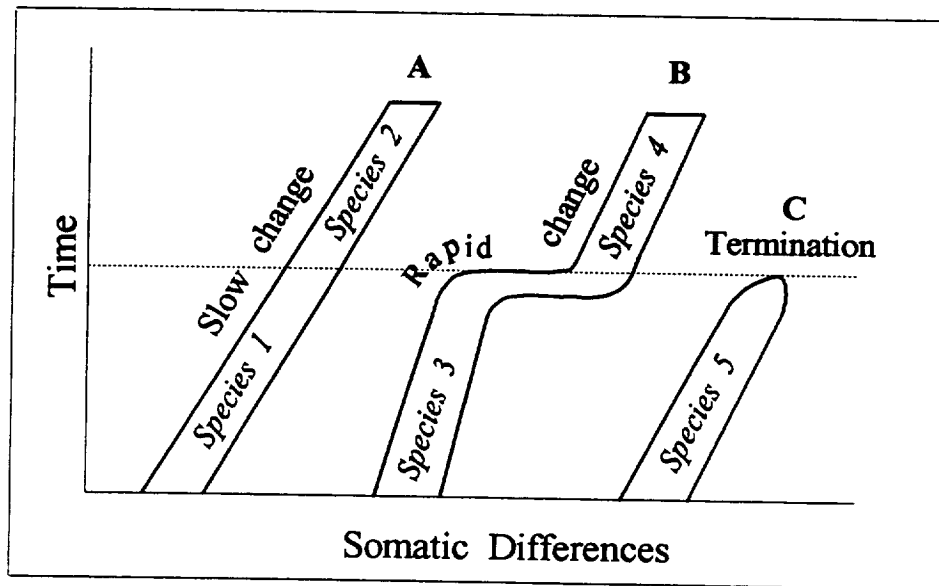

Figure 1. Three types of species extinction events. A, B. Geologically slow and rapid pseudoextinction events with a genetic continuum between the two species in each lineage. C. Terminal species extinction event results in the truncation of lineage (Modified from Simpson, 1983).

RATES OF EXTINCTION

The rate of extinction has been divided into two categories: **background** and **mass extinction** (Figure 2). During the Phanerozoic, there have been extended periods when some taxa became extinct, but others appeared in approximately equal numbers. This has been termed background extinction. The total number of species in the biosphere remains more or less constant for a given interval of time. Mass extinction, however, encompasses periods when the numbers of taxa becoming extinct far exceeds the new species appearing, resulting in a reduction of diversity in the biosphere.
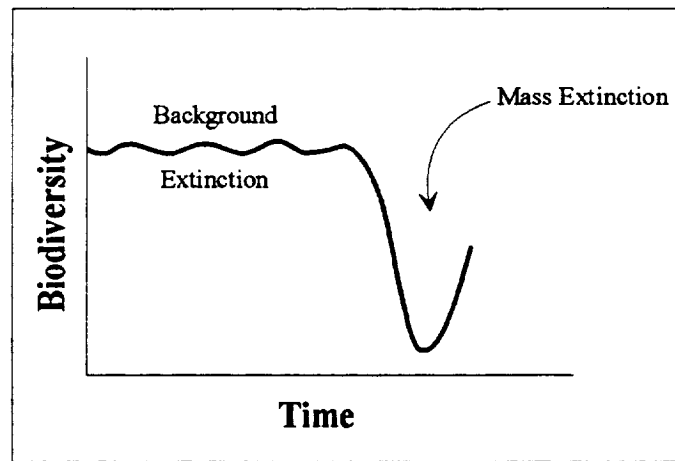
Figure 2. Relationship of global biodiversity to continuous background extinction and to a profound mass extinction event.

The phenomenon of mass extinction may be subdivided into two categories (Figure 3), depending on the rate of extinction. **Accelerating mass extinction** is defined as occurring over a geologically short period of time such as 10's, 100's of thousands, or a million or so years. **Instantaneous catastrophic mass extinction** is virtually instantaneous, occurring over a period of only days, weeks, months or, at most, a few years.
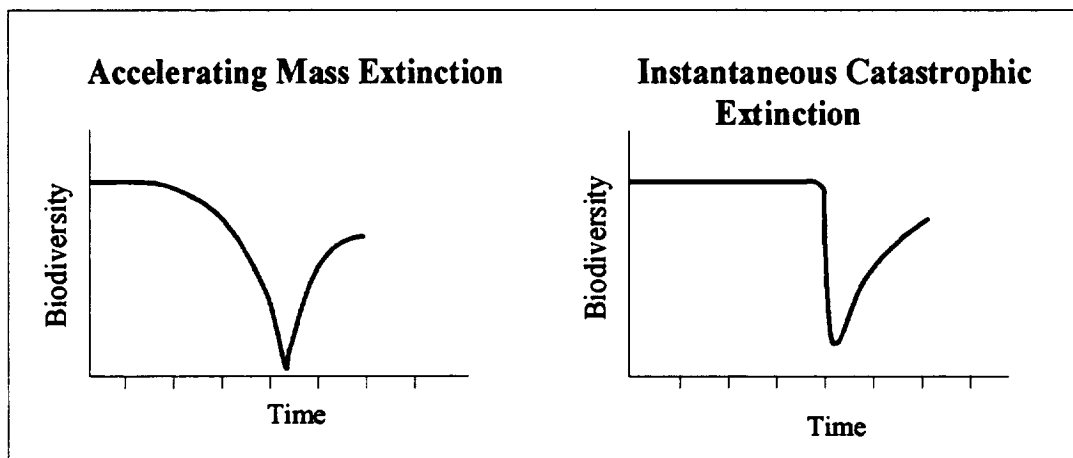

Figure 3. Relationship of length of mass extinction events to the decline in global biodiversity.

Since mass extinction can be either geologically short and gradual or catastrophic and instantaneous, the problem lies in an ability to differentiate between these short-term events. The farther back in time we go the greater the difficulty of distinguishing small increments of time. Because of this inability, it becomes difficult to distinguish between accelerated and catastrophic extinctions.

CYCLICITY OF MASS EXTINCTION

It long has been known, beginning with Cuvier's description of catastrophes, that the geologic record is punctuated by episodes of mass extinction. Analyses of changes in biotic diversity during the Phanerozoic (Raup and Sepkoski, 1985, 1986) suggest that these extinction events were cyclic, with a periodicity of approximately 26 million years. Although the intensity of these periods of mass extinction and the groups of organisms being affected vary from one event to another, the periodic reoccurrence of mass extinction has played an important role in the evolution of Earth's biota. The apparent cyclicity of mass extinction events also raises the possibility of an underlying abiotic cause.

WHAT CAN THE FOSSIL RECORD TELL US ABOUT EITHER OF THESE TWO COMPETING HYPOTHESES?

In examining the TCEE in the context of either the impact or the volcanic hypotheses, it is essential to remember that even though the end results are similar, the rates of the "great dying" will differ. If the TCEE was a consequence of an impact, it would have been catastrophic and marked by an extirpation horizon marking the event. Even if we grant that most of debris of the impact holocaust was subsequently erased by erosion, one would still expect to encounter areas where the charred and twisted dinosaur bones are preserved, or areas of seafloor characterized by a single, iridium-enriched layer of sediments packed with the remains of the victims of the impact, such as ammonites, mosasaurs, pleisosaurs and other marine organisms. No such horizon at the K/T boundary has been documented conclusively in the field. Such "horizons of death" resulting from local catastrophic events are known throughout the geologic record. Horner (1988) has reported a single bed in the Upper Cretaceous that extends for miles and contains an estimated 10,000 individual Maiasaurus killed during a nearby volcanic eruption. The question can be asked: if a thin layer of iridium can be preserved at the K/T boundary, where are the bodies?

The biotic consequence of volcanically induced environmental disruption would be characterized by a period of accelerated mass extinction and should not be marked by a single extripation. Because such extinction would have occurred over a period that coincided with the waxing and waning of volcanic activity, it would be expected that victims also would be distributed through an interval of sedimentary rocks rather than concentrated into a single layer.

Initial data presented by proponents of the asteroid theory purported to show "extripation horizons" that affected a variety of types of organisms (Figure 4A), but these horizons of extinction are, in fact, known only from the literature. Kauffman (1984) presented an elegant discussion showing that the precision alluded to in the literature is generally not sufficient to substantiate catastrophic extinction events. Kauffman cites a number of examples to illustrate that, upon closer examination, many taxa previously considered as extinct at the K/T boundary actually disappeared prior to the final stage of the

Cretaceous, the Maastrichtian (Figure 4B). Kauffman also pointed out that one of the complicating factors in our understanding of the TCEE was a global sea-level regression that destroyed most nearshore environments, and, thus, has greatly limited the opportunity to study this interval of time.
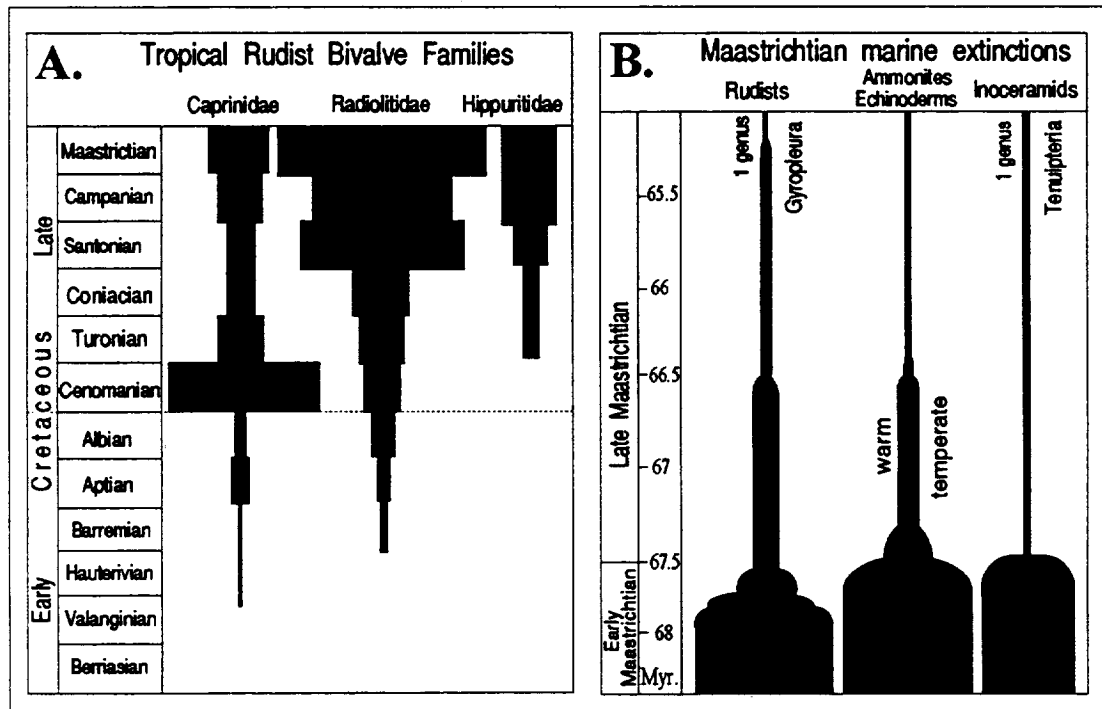

Figure 4. A. Apparent K/T extirpation horizon as commonly portrayed in the literature. The practice of extending the ranges of taxa to stage boundaries invariably results in "pseudo mass extinction horizons." Modified from Kauffman (1984). B. Detailed plotting of the biostratigraphic distribution of selected groups of Late Maastrichtian mollusks and echinoderms reveals that most of the extinction occurred well before the end of the Cretaceous. Modified from Kauffman (1988) and Ward (1991).

However, even cursory inspection of earlier data reveals several interesting features of biotic changes prior to the K/T event that need to be addressed by proponents of the impact and volcanism hypotheses. One of these is the apparent occurrence of several periods of apparent extinction approaching an extinction event. Because these data did not conform to an instantaneous catastrophe, proponents developed the Stepwise Extinction Model based on multiple impacts events or comet showers (Hutt et al., 1987). This pattern also could be explained by the atmospheric effects of waxing and waning of volcanic activity.

The gradual decline in diversity has long been known among many groups such as ammonites and dinosaurs, prior to becoming extinct at the end of the Cretaceous.

Although the cause of this decline has not been explained to everyone's satisfaction, the phenomenon cannot ignored, and may be very important. Another factor, not commonly recognized until recently, is the diachronous (non-synchronous) geographic disappearance of some important marine groups during the Late Cretaceous. Work in the polar regions during the past two decades has greatly increased biogeographic knowledge of life in the high southern latitudes during the Late Cretaceous and Early Tertiary (see Feldmann and Woodburne, 1988). Extensive field work and study of the latest Cretaceous molluscan faunas from Antarctica (Zinsmeister et al., 1989) has shown that the decline and disappearance of some typical Cretaceous marine invertebrates, such as belemnites and inoceramids, occurred much earlier in the high southern latitudes. Belemnites disappear in the Antarctic during the latest Campanian or earliest Maastrichtian (Doyle and Zinsmeister, 1988) but survived until the latest Maastrichtian in the mid and lower latitudes. Inoceramid bivalves show a similar pattern with the last inoceramids occurring in the Campanian (Crame, 1983), though surviving to the end of the Cretaceous in lower latitudes. This diachronous pattern of geographic disappearance suggests that a fundamental biologic or climatic factor is at work, which eventually led to the extinction of these groups.

SELECTIVE NATURE OF THE TERMINAL EXTINCTION EVENT

One feature conveniently overlooked by proponents of the impact hypothesis is the selective nature of the Terminal Cretaceous Extinction Event. One basic tenant of the impact hypothesis was that the food chain was severely disrupted by the loss of the photosynthesizing producers at the base of the chain; this led a to chain-reaction of death and extinction by starvation in the higher levels of the food chain. This was the principal argument for the extinction of large terrestrial tetrapods, and the disappearance of marine organisms such as ammonites and marine reptiles. Surprisingly, a number of nektonic organisms, such as bony fishes and sharks, which presumably occupied the same levels in the food chain as the ammonites and marine reptiles, did not become extinct. The question might again be asked, why should the bony fishes and sharks, which presumably occupied the same levels in the food chain, survive and not the ammonites and marine reptiles?

If the "Night of the Living Dead" scenario is correct, all environmentally-sensitive groups should have been greatly affected. Once again the selective nature of the K/T extinction becomes apparent. Although reef building rudist bivalves appeared extinct at the end of the Cretaceous, modern reef building scleractinian corals survived virtually unaffected. Because of the poor Late Cretaceous fossil record, birds are commonly dismissed in discussions of the TCEE. Birds are particularly sensitive to environmental disruption and their survival of the mass extinction at the end of the Cretaceous cannot simply be dismissed from any discussion of the TCEE on the grounds of a poor fossil record. Simply dismissing an important group such as the birds from the discussion of the TCEE because of a limited fossil record is not the way to do science!

BIOSTRATIGRAPHIC PATTERNS OF EXTINCTION EVENTS

The disappearance of species in the fossil record during an extinction event will leave a biostratigraphic pattern which should provide data about the causes. Each of the hypotheses that have been proposed should leave a characteristic biostratigraphic signature that should be recognizable by utilizing high resolution stratigraphic techniques. It should be noted that K/T sections that are characterized by a great reduction in sedimentation rates, or by hiatuses, are not useful in high resolution stratigraphic studies because critical biostratigraphic range data are masked and will appear as pseudo-extinction horizons (Figure 5). Those sections that are characterized by relatively rapid and continuous sedimentation should be studied in detail, because
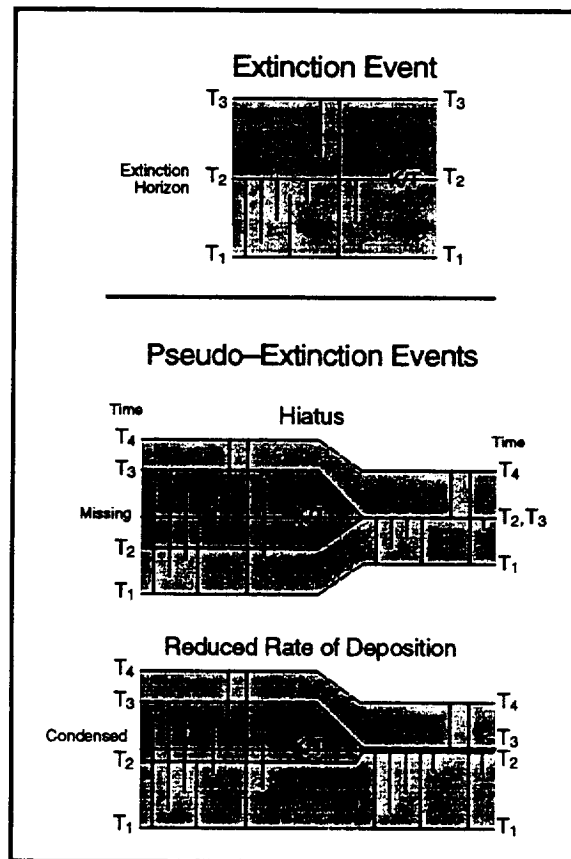

Figure 5. Pseudo-extinction horizons may be produced by a hiatus resulting in a gap in the stratigraphic record or in a condensed section where the rate of deposition was greatly reduced. In either case, species ranges are truncated giving the appearance of an mass extinction event.

these are sections that will preserve accurate records of biotic events at the end of the Cretaceous and, perhaps, also reveal post-extinction events. With high-resolution stratigraphic techniques, it should be possible to recognize which of these fossil signatures is present.

CONCLUSION

The selective use and forcing of data to support catastrophic scenarios for the extinction of the dinosaurs and other mass extinction at the end of the Cretaceous has hindered our quest to understand the cause or causes of an event that drastically altered the biosphere 65 mya. Feldmann (1990) has pointed out that the polarized nature of the debate has reversed the normal scientific method of testing new hypotheses by putting the burden of proof, not on the proponents of impact, but on those questioning the impact hypothesis. Speculations about the impact event and after-effects have been "elevated to an article of faith." The fundamental problem in the debate has been a failure to distinguish between the need to prove the actuality of the impact event, and demonstrating that it was the underlying cause of the TECC. The assumption is made that demonstration of the impact occurrence was de facto proof that it was the primary cause of the TECC. Our understanding of the biotic events at the end of the Cretaceous neither can, nor will, rest solely on the physical evidence of the impact or volcanic catastrophe, but must rest ultimately on the paleontologic record.

The accumulation of several kinds of physical evidence indicates both that an impact of major proportions probably did occur at the end of the Cretaceous, and that it was also a time of massive volcanic activity. Both events would have had a drastic affect on the Earth's biosphere. The major difference between the two is in the rate of environmental disruption leading to the TCEE. The utilization of high resolution, species level biostratigraphic studies of stratigraphic sections characterized by continuous, uninterrupted deposition will reveal extinction patterns which eventually will lead to a better understanding of the cause or causes of one of the most profound events in the history of life.
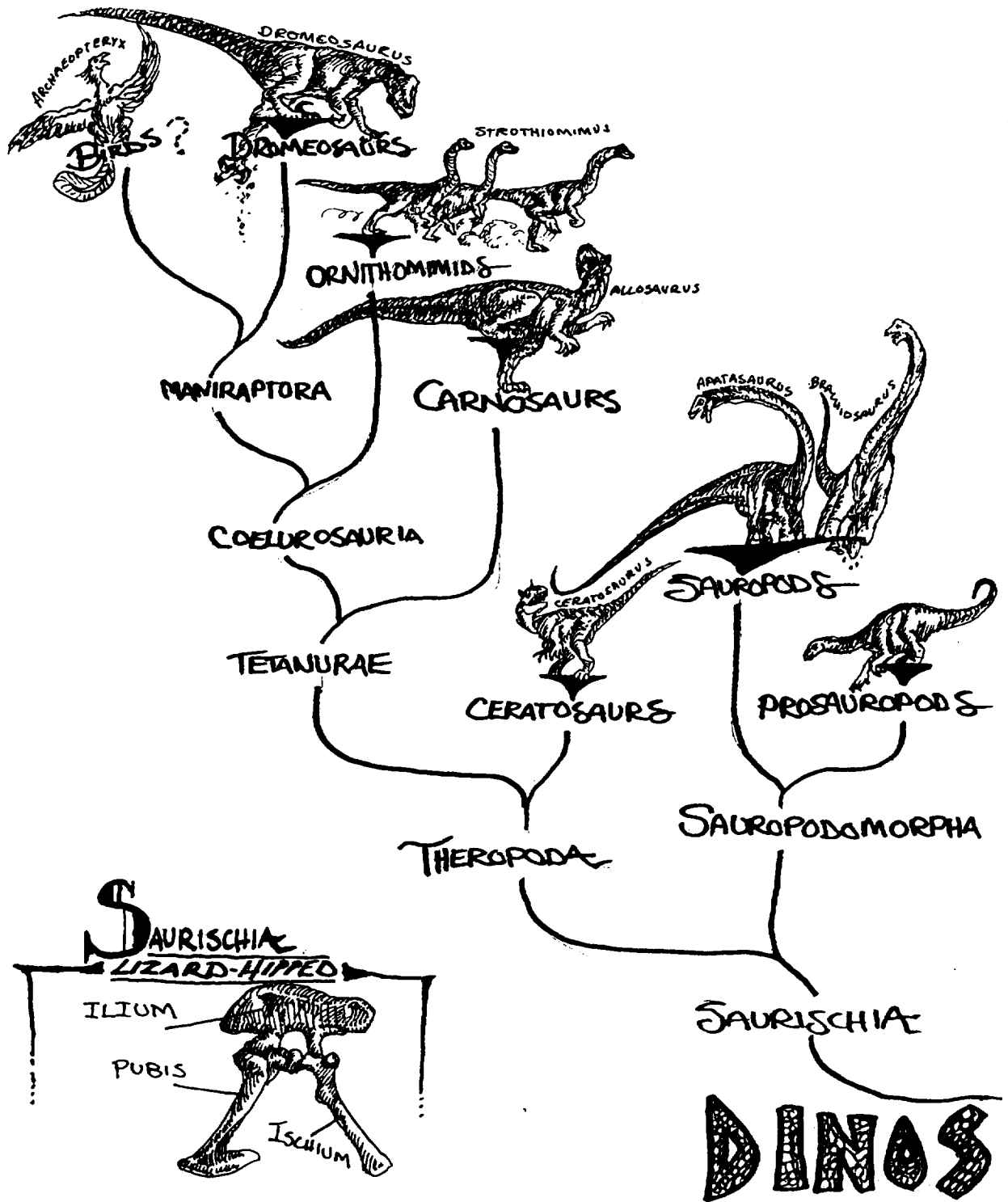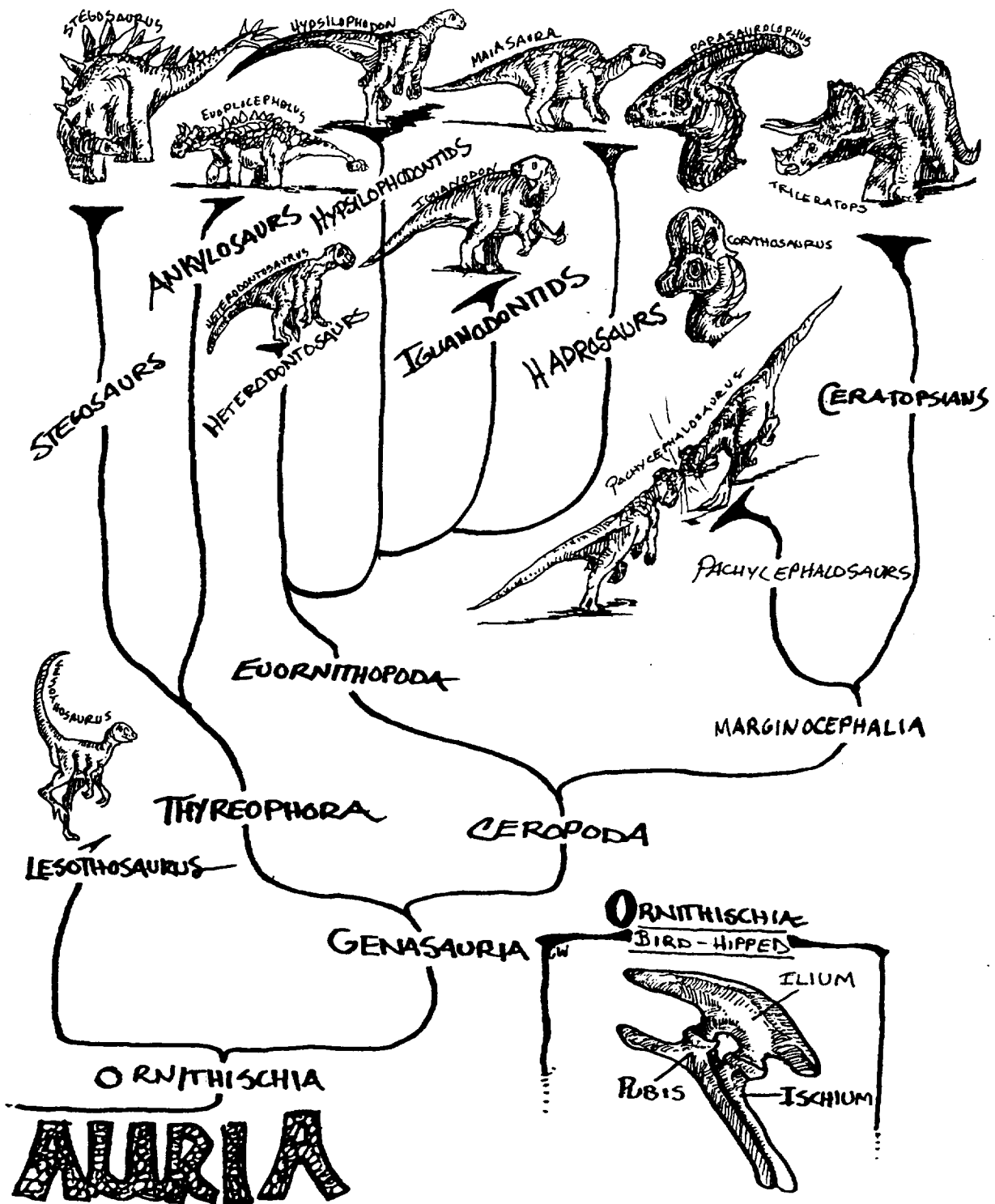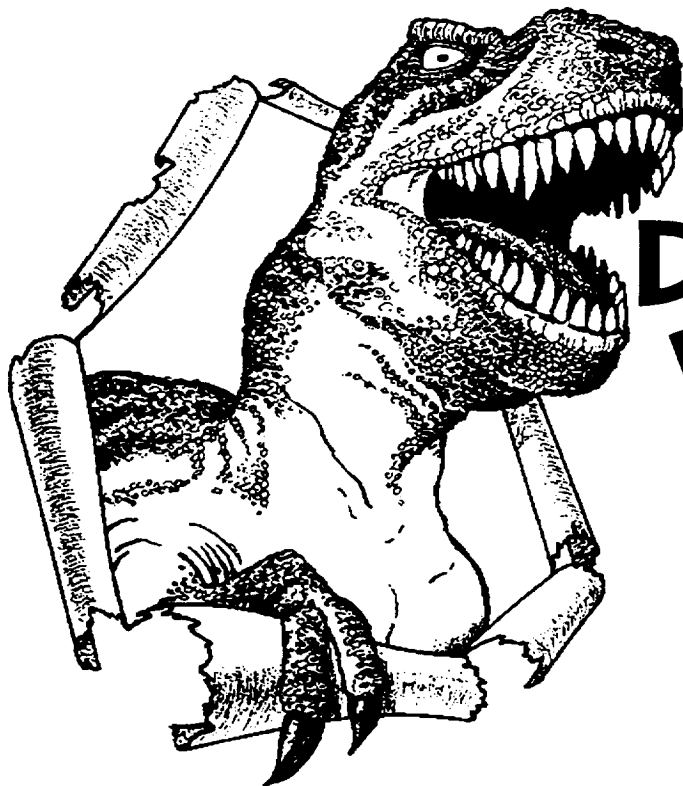
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ARCHAEOPTERYX

DROMEOSAURUS

BIRDS?

DROMEOSAURS

STROTHIOMIMUS

ORNITHOMIMIDS

ALLOSAURUS

MANIRAPTORA

CARNOSAURS

APATASAURUS   BRACHIOSAURUS

COELUROSAURIA

CERATOSAURUS

SAUROPODS

TETANURAE

CERATOSAURS

PROSAUROPODS

THEROPODA

SAUROPODOMORPHA

SAURISCHIA
LIZARD-HIPPED

ILIUM

PUBIS

ISCHIUM

SAURISCHIA

DINOS

Courtesy Colin Whitfield

THE DINOSAURS WERE HERE!

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